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THE DIFFERENTIATION OF THE EGGS OF THE TRICHOSTRONGYLID SPECIES *NEMATODIRUS FILICOLLIS* AND *N. SPATHIGER*

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In his description of species of *Nematodirus* May (1921) was unable to distinguish clearly between the females of species; two of these were *N. filicollis* and *N. spathiger*. Among characters which he considered, were dimensions of eggs, and these were found to overlap between species. Thus he records for the eggs of *N. filicollis* a range of 130–200 μ in length by 70–90 μ in width and for *N. spathiger,* respectively 150–220 μ and 80–110 μ. Tetley (1935) pointed out that if attention were paid to dimensions embracing the greater number of eggs of these species, specific differences could be observed, for the majority of the eggs of *N. filicollis* were grouped within the limits of 140–165 μ by 70–85 μ and those of *N. spathiger* within 180–210 μ by 90–105 μ. Shorb (1940) found that the dimensions for *N. filicollis* ranged from 147.2–195.7 μ by 72.8–108.3 μ. From the measurements he has plotted, though small in number, it is apparent that the majority fell nearer the lower limits of this range.

A female of *Nematodirus* has been found in which the eggs of each uterus, respectively, fell centrally in the *N. filicollis* and *N. spathiger* groupings. While this is regarded as exceptional, it is considered that in view of the possible use of egg measurements in specific identification of females of this genus, the evidence providing the basis for previous conclusions, together with more recent findings, should be made known.

MATERIALS AND METHODS

Material for measurement was obtained mainly from the dissection of females; the data pertaining to fecal eggs were collected in the course of applying the Stoll dilution egg counting method. Eggs dissected from females were measured as soon as possible after removal of worms from

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the sheep at autopsy, this sometimes involving a delay of some hours. Fecal eggs, as a rule, were exposed to the action of N/10 NaOH for several hours. Some material was fixed in hot 5 per cent formalin within a few moments of the death of the host. The specific numbers of males of *N. filicollis* and *N. spathiger* were taken as indices of the numbers of females of the two species. Measurements were made using an ocular micrometer.

OBSERVATIONS

Sheep I.

Breed: Romney cross.
Age: approximately three months.
Slaughtering date: December 7, 1932.
Place of origin: Palmerston North, New Zealand.

Two hundred males of *Nematodirus* were examined; these were found to consist of 199 *N. filicollis* and 1 *N. spathiger*. Measurements were made of 101 eggs dissected from 7 worms selected at random. The results are plotted in Fig. 1.

Sheep II.

Breed: Romney cross.
Age: four months.
Slaughtering date: May 21, 1936.
Place of origin: Palmerston North, New Zealand.

This animal was slaughtered in an advanced state of exhaustion, the outcome of parasitic gastritis. Material was fixed in hot 5 per cent formalin. The infection of *Nematodirus* was drawing to a close, as shown by the scattering of parasites throughout the digestive tract from the duodenum to the rectum. Males of *N. filicollis* and *N. spathiger* were present in approximately similar numbers. From each of 62 females taken at random at least one representative egg was extracted. These and eggs found free in the lumen of the digestive tract, were measured, 119 of which measurements are plotted in Fig. 2. Abnormal eggs found in this material have been omitted from Fig. 2 and are discussed in another part of the paper.

Sheep III.

Breed: not known.
Age: a few months old.
Slaughtering date: November 15, 1939.
Place of origin: Topeka, Kansas.

Examination of 40 males of *Nematodirus* resulted in finding 37 of *N. spathiger* and 3 of *N. abnormalis*. Forty females taken at random were found on cursory examination to contain eggs of uniform shape

and size; of these, 20, again selected at random, were dissected and one typical looking egg from each measured. The results are plotted in Fig. 3.

Sheep IV.

Breed: Southdown Romney cross.
Age: approximately twelve months.
Dates of fecal examination: during 1935.
Place of origin: Palmerston North, New Zealand.

The data were derived from eggs encountered while making dilution fecal counts by the Stoll technique. These are plotted in Fig. 4. Post-mortem examination was not made, but from autopsies on other animals reared in the same paddock it was found that *N. filicollis* and *N. spathiger* were abundant while *N. abnormalis* and *N. helvetianus* were rarely present and then only as odd individuals.

Aggregated Results

In addition to the foregoing data, the series was enlarged through the study of eggs from other worms, obtained from Romney cross lambs located at Palmerston North. In Fig. 5, the measurements of 280 of these are graphed, together with the 279 already shown from sheep 1–4, as a total sample of 559.

To indicate something of the range of experience contained in the results, the dates and places of origin, number of sheep providing material, and the numbers of worms dissected are set out in Table 1.

TABLE 1. *Sources of material*

Origin		Number of sheep providing material	Source of eggs: Number of worms
Date	Place		
1932 Nov.	Palmerston N., N. Z.	1	1
" Dec.	" " "	1	1 (See Fig. 1)
1934 Nov.	" " "	2	2
" Dec.	" " "	3	3
1936 May	" " "	1	62 (See Fig. 2)
1938 Jan.	" " "	1	3
" Feb.	" " "	3	19
1939 Nov.	Topeka, Kans.	1	20 (See Fig. 3)
1935 } 1936 }	Palmerston N., N. Z.	1	Feces (See Fig. 4)
Total		14	111 (at least)

Irregularities in Dimension of Eggs

Occasionally when examining fecal material abnormally small *Nematodirus* eggs were found and, once, an infection (sheep II) was found in which females contained eggs of irregular dimensions. Among 62 females from this latter source 8 contained eggs which departed in one or more respects from the normal. One worm was found to contain eggs of differing dimensions between the two uteri. Thus, of the 7 uni-

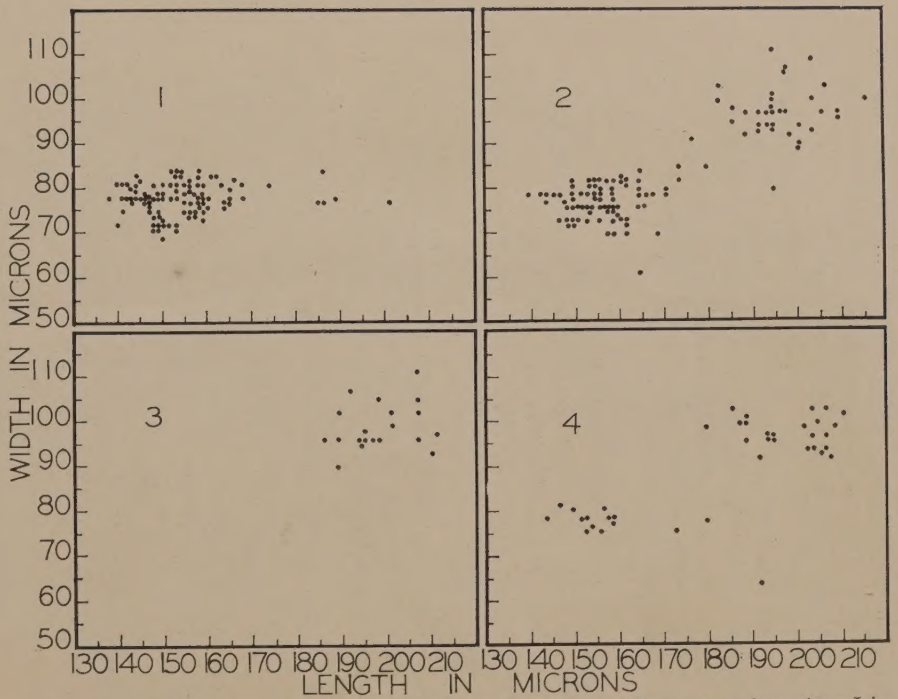

FIG. 1. The dimensional frequency distribution of eggs dissected from worms from sheep I in which *N. filicollis* males predominated in the ratio of 199 : 1 over those of *N. spathiger*.

FIG. 2. The dimensional frequency of eggs dissected from worms from sheep II in which males of *N. spathiger* and *N. filicollis* were in approximately similar numbers.

FIG. 3. The dimensional frequency distribution of eggs dissected from worms from sheep III in which males of *N. spathiger* were present and those of *N. filicollis* absent.

FIG. 4. The dimensional frequency distribution of fecal eggs from sheep IV. See text.

form eggs of the anterior uterus, there were 6 with the dimensions: 195 × 85 μ, 195 × 93 μ, 198 × 93 μ, 192 × 96 μ, 192 × 99 μ, 198 × 90 μ; and among the equally uniform eggs of the posterior uterus 6 were of the following sizes: 171 × 78 μ, 168 × 78 μ, 160 × 81 μ, 171 × 81 μ, 168 × 81 μ, 180 × 81 μ.

Each of the remaining 7 worms, exhibiting irregularities, contained one or more abnormal eggs sandwiched between seemingly normal eggs.

It was apparent, from the degree of segmentation and number of eggs, that egg production by the 8 females was below that of other members of the population among which, in turn, the rate fell below the normal for the species. Malformed eggs were not to be found among the 1,024 eggs found free in the contents of the alimentary canal of sheep II.

DISCUSSION

Eggs of *Nematodirus* species, partly on account of their thick resistant shells, are not readily subject to change in shape and volume through fluctuations in osmotic or mechanical pressure. The similarity of the results for dissected out eggs (Figs. 1, 2 and 3) to those for fecal eggs (Fig. 4) was therefore not unexpected.

It is seen from Figs. 1, 2, 3, 4, and 5 that two distinct groupings of eggs were present; the obvious conclusion is that two species were con-

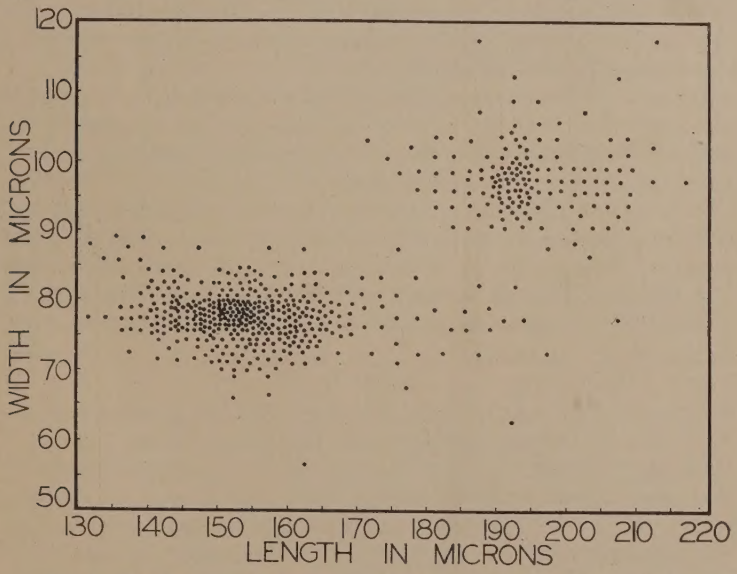

FIG. 5. The dimensional frequency distribution of *Nematodirus* eggs from all sources, including those in Figs. 1–4, supplemented by 280 others. It will be seen that the identity of the specific groupings is distinct.

cerned. Males of species other than *N. filicollis* and *N. spathiger* were so rarely found that the other species will be disregarded as insignificant in the present discussion. There can be no doubt therefore that the groupings were of *N. filicollis* and *N. spathiger*.

In sheep I the finding of males in the proportion of 199 of *N. filicollis* to 1 *N. spathiger* indicated the probability that females taken for dissection were of *N. filicollis*. The data from this sheep (Fig. 1) reveal that there was a dimensional range among the eggs of 138–201 μ by 69–84 μ.

The even division of the males of the two species, *N. filicollis* and *N. spathiger*, observed by inspection in sheep II, is reflected in the two groupings of the eggs dissected from this animal (Fig. 2). One grouping, 140–170 μ by 61–85 μ, coincided with that found in sheep I and it is concluded was of *N. filicollis*. That the second grouping, 180–215 μ by 85–110 μ, was *N. spathiger* is clinched by the results from sheep III (Fig. 3). A sample population from this animal contained 37 males of *N. spathiger* to 3 of *N. abnormalis*, and this, it is believed, indicated that *N. filicollis* was absent. The range of egg measurements, therefore, found in this animal, of 185–210 μ by 90–110 μ finally established that the eggs of the two species under discussion were distinct in size.

The results from sheep IV (Fig. 4) show that the groupings were distinct among eggs of fecal origin; and the aggregated results (Fig. 5) indicate that despite the miscellaneous origin of the data the groupings retained their identity. It is therefore concluded that the differences found were of general occurrence.

In view of the centering tendency found in the data, it was considered that a statistical treatment in which attention was paid to range of distribution in conjunction with intensity of population would enable interspecific differences to be more clearly demonstrated.

The specific population groups were regarded as resembling a bivariate normal frequency distribution sufficiently closely to permit the application of formulae relevant to the latter. Thus the range of the mean plus and minus twice the standard deviation which, in a universe, would enclose 91.2 per cent of the population, was estimated for the data from sheep I and the aggregated data for the arbitrarily defined specific populations. These ranges, to the nearest micron, are given in Table 2. It can be seen, for *N. filicollis*, that the range for sheep I closely approximated that for the aggregated results. This would indicate that only a small degree of inter-host fluctuation in the size of eggs of this species took place. While data, equivalent in every respect, were not available for *N. spathiger*, there was no reason for suspecting that a different state of affairs obtained for this species. It was considered, therefore, that statistical comparison of the populations of *N. filicollis* and *N. spathiger* could be reasonably made.

TABLE 2.—*The mean axial lengths of eggs of* Nematodirus filicollis *and* N. spathiger *and the computed range of distribution of 91.2 per cent of their populations*

Species	Means		Distribution of 91.2% of eggs[c]	
	Length μ	Width μ	Length μ	Width μ
N. filicollis[a]	154.55 ± 0.71	77.47 ± 0.23	133–176	71– 84
N. filicollis[b]	153.92 ± 0.34	77.16 ± 0.14	134–174	69– 86
N. spathiger[b]	194.64 ± 0.44	97.27 ± 0.44	179–210	88–107

[a] From sheep I.
[b] From aggregated results (see Fig. 5).
[c] The statistical range of the mean plus and minus twice the standard deviation.

The ranges of distribution of 91.2 per cent of the populations of *N. filicollis* and *N. spathiger* are seen in Table 2 not to have overlapped. In that these ranges were separated and that only a fraction of the populations of the outer statistical zone (containing 8.8 per cent of populations) overlay one another, the individual chances of eggs of one species falling within the 91.2 per cent zone of the other, were small. The partial overlapping of the outer zones of quadrants of the distributions reduced individual chances of falling within the extreme range of the second species, to within the vicinity of one in forty; the individual chances of falling within the statistical range of 91.2 per cent of the other species were much smaller. It is therefore considered that the range of 91.2 per cent of the populations may be regarded as a specific character so far as *N. filicollis* and *N. spathiger* are concerned.

Possibly in other instances where specific differences between females have not been clearly apparent this method of identification may have application.

It is concluded that the malformed eggs were, from the point of view of the present discussion, of little significance. However, as the host in which these were found was in a state of extreme exhaustion at the time of death and as many of the parasites were in the act of being eliminated, it is possible that they have significance as an expression of a phase of the host-parasite relationship adverse to the parasite species. The finding of even a few malformed eggs would, in this connection, be of importance.

SUMMARY

By plotting lengths against widths it was possible to distinguish between the eggs of *Nematodirus filicollis* and *N. spathiger*.

The extreme ranges of the respective bivariate normal frequency distributions overlapped but this did not happen within the statistical ranges of means plus and minus twice the standard deviations.

Ranges so computed were, for *N. filicollis*, 133–176 μ by 69–86 μ and for *N. spathiger*, 179–210 μ by 88–107 μ.

In that these ranges were estimated to enclose 91.2 per cent of the

populations of the two species it is suggested that they have value in the specific identification of females of the two species.

It is further suggested that the method may have wider application in the identification of species where specific differences between females by means of other characters have not been clearly demonstrated.

The finding of even a small number of malformed eggs in the feces of a host, it is concluded, is an index of a pitch of the host-parasite relationship, adverse to the parasite.

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THE EGG-LAYING FUNCTION OF A NEMATODE AS SHOWN BY STUDY OF *NEMATODIRUS* EGGS IN UTERO

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At present, methods do not exist for measuring exactly the pitch of the host-parasite relationship at one point of time. Vague indications of the potential of the relationship have been obtained by observing (1) the ability of parasites to survive, (2) the size to which parasites have grown, (3) the effects of the parasites on the host over a period of time, (4) the feeding of the parasites, and (5) the fecundity of parasites as shown by fecal egg numbers, these latter being expressed either as an empirical figure or as a mean for the population.

The degree to which the various functions of the parasites are related to those of the host-parasite relationship seems still to be largely unknown. It would be expected that they would be linked. Thus, in connection with egg-laying of many parasites, from the standpoint of quantity of eggs produced, or the total bulk of such eggs, it would appear that egg-laying has a relationship to the feeding of the worms, proceeding either simultaneously or alternately at short intervals, with feeding. To the extent therefore that extraction of food from the host is responsible for the effects, fecundity must be regarded as an index of these effects. Support for this is provided by Stoll and Tseng (1925), who found that the production of eggs by hookworms, indicated by per gram fecal counts, paralleled clinical symptoms of disease caused by these parasites as measured by lowered hemoglobin or blood loss. Then again from the viewpoint of host resistance or the favorability of the host for the parasite, egg production has been used as an index. Stoll (1929), with *Haemonchus contortus,* the same author (1932) and Sarles (1932), with *Trichostrongylus calcaratus,* were early in the field to investigate the host-parasite relationship by following the egg production of parasites.

In the belief, therefore, that closer study of egg production by parasites would result in knowledge that might aid in the measurement of the pitch of the host-parasite relationship, an examination has been made of the uterine egg populations of *Nematodirus* species in sheep.

Graham (1938) has investigated the fecundity over a period, of single individuals of *Strongyloides ratti.* The present approach, in essentials, is complementary to this work in that the egg output of whole populations at one point of time has been considered.

Nematodirus species were found a convenient experimental medium.

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The eggs of *N. filicollis* and *N. spathiger* are easily distinguishable from one another and from those of other genera; their numbers in utero are relatively small, though sufficiently numerous for effective statistical treatment; counting of cells is particularly easy in the eggs of this genus for segmentation rarely proceeds beyond the 8-cell stage in the host, and up to and including the 16-cell stage, at least, the comparatively large cells, resulting from holoblastic equal division, retain a clear-cut spherical form; eggs are laid in the order in which they are produced by the ovaries. Species were easily procured in abundance.

MATERIAL AND METHODS

Material was obtained from Romney cross lambs at Palmerston North, New Zealand.

Following slaughtering of the lambs, material was removed within the space of a few minutes and fixed in hot 5 per cent formalin in order to kill eggs, both within the worms and free in the ingesta.

Examination for the numbers and degree of segmentation of eggs was made on the intact worms, using a dissecting microscope.

Specific identification of females was accomplished from characters of the contained eggs (Tetley, 1935).

RESULTS

Data were obtained from five sheep. Numbers I, II, III and IV were spring-born lambs approximately four months of age and in good health at the time of slaughtering; sheep V was a summer-born lamb, also about four months of age at the time of autopsy, but in an exhausted condition as the result of parasitic gastritis. Populations of *N. filicollis* and *N. spathiger* were located, in all five animals, mainly in the anterior part of the small intestine. It was apparent that the infection was in process of being eliminated in sheep V, as parasites were scattered along the whole length of the alimentary canal posterior to the duodenum.

Material was taken from the small intestine of the first four animals without regard to the region of infection. In the instance of sheep V note was made of the section of the alimentary tract from which samples were taken. The accompanying tabulation indicates the number and origin of the female worms providing in utero data.

Sheep	Region of digestive tract	*N. filicollis*	*N. spathiger*
I	Small intestine	18	6
II	" "	15	10
III	" "	31	1
IV	" "	14	5
V	7–12 feet	40	13
	25–30 "	9	30
	31–36 "	5	30
	37–42 "	–	19
	43–48 "	8	36
	Cecum	–	26

Complete data on numbers and degree of segmentation of eggs were collected for the majority of worms above listed. In others the maximum degree of segmentation only was observed.

A condensation of the data is set out as follows:

Table 1. The frequency with which worms contained arrays of the various segmentation stages of eggs.

Table 2. The frequency with which segmentation stages of eggs were found as maxima for individual uteri.

Table 3. The relative frequency of segmentation stages of eggs of *N. filicollis* and *N. spathiger* found free in the lumen of sections of the alimentary canal of sheep V at the time of autopsy.

Table 4. The mean frequencies of segmentation stages of eggs in utero.

Table 5. The frequency with which one or other uterus predominated in number of unsegmented eggs.

Table 6. The frequency of uteri containing unsegmented eggs.

Table 7. The frequency of the numbers of unsegmented eggs in individual worms.

Fig. 1. The correlation between the anterior and the posterior uteri of individuals of *N. filicollis* in the numbers of unsegmented eggs.

Fig. 2. The correlation between the numbers of unsegmented and 2-cell *N. filicollis* eggs in utero.

The Segmentation of Eggs

On account of the small area of cross section of the lumen of the genital tract, eggs of *Nematodirus* species proceed along its entire length in single file. Thus they come to be laid in the order of their origin in the ovary. Eggs of the anterior uterus may be crowded sometimes, and tend to lose this order; the disruption, however, does not extend as far back as the 2-cell stages. Among the several hundred worms examined, in only one female of *N. filicollis* was the serial order of the eggs lost. This female contained an abnormally large number of eggs in both uteri.

Following entry of eggs to the uterus and fertilization, segmentation begins, the successive cleavages taking place in the order of extrusion of the eggs from the ovary. In this way particular segmentation stages come to be grouped together. Departures from this sequence were rare. Among a total of 108 females of *N. filicollis* and 54 *N. spathiger* from sheep I, II, III, IV and V there were 6 worms of the former species and 2 of the latter in which odd eggs were out of the normal segmentation order. In 3 of the *N. filicollis* females the interruption was associated with obvious size abnormality on the part of the displaced eggs. The remaining instances concerned normal eggs which were located among the next higher segmentation stage. These it is considered were examples of extreme fluctuation that might be expected to occur in the length of time of the various stages.

From the synchronous division of cells in individual eggs and the orderliness of the array of segmentation stages along the uterus it is concluded that the extrusion of successive eggs from the ovaries was at intervals of sufficient length to mask individual fluctuations in time of fertilization and in lengths of the succeeding cleavages.

The Stage of Segmentation at Which Eggs are Laid and the Development of Eggs in the Alimentary Canal

The range of the maximum stages of segmentation found in individual worms and the frequencies of the various segmentation stages found in the lumen of the alimentary canal are set out in Tables 2 and 3. From these it is concluded that eggs were being laid by worms at the 2–8-cell stages, in both *N. filicollis* and *N. spathiger* the 3–4-cell stage being the one at which most worms were laying eggs.

The frequently recorded fact that eggs of *Nematodirus* are voided in

TABLE 1.—*The frequency of arrays of segmentation stages in populations of* N. filicollis *and* N. spathiger. *An unbroken array has been regarded as one in which all intermediate cleavage stages between unsegmented eggs and the maximum stage found in a uterus, were present*

Species	Sheep	Frequency of array					
		Anterior uterus			Posterior uterus		
		Unbroken	Broken	No eggs	Unbroken	Broken	No eggs
N. filicollis	I	17	1	–	18	–	–
" "	II	13	1	–	14	–	–
" "	III	30	–	1	31	–	–
" "	IV	14	–	–	13	–	1
" "	V	25	3	–	19	9	–
N. spathiger	I	6	–	–	6	–	–
" "	II	10	–	–	10	–	–
" "	III	1	–	–	1	–	–
" "	IV	4	–	–	4	–	–
" "	V	27	2	1	28	1	1

the feces of the host in the 8-cell stage was confirmed. Occasionally eggs in earlier stages of segmentation were found in feces and once a 16-cell egg was found in material removed at autopsy and fixed with heat within a few moments of the death of the host.

In Table 3 comparison has been made of the percentages for each stage of egg-segmentation of *N. filicollis* and *N. spathiger* from various sections of the digestive tract. The greater part of the populations of these two species was located in the anterior region of the small intestine; therefore the comparison was essentially of eggs that had traversed almost the entire length of the small intestine. It is seen that the percentage of 1–4-cell stages diminished with passage along the intestine, from 68 per cent to 30 per cent in the instance of *N. filicollis* and 61 per cent to 13 per cent in *N. spathiger*. The conclusion is drawn that during the time of this passage many eggs graduated to the 8-cell stage but that no 8-cell

TABLE 2.—*The frequency with which segmentation stages of eggs were found as maxima for individual uteri*

Sheep	Maximal segmentation class									
	Anterior uterus					Posterior uterus				
	0[a]	1	2	3–4	5–8	0[a]	1	2	3–4	5–8
	N. filicollis									
I	–	2	2	8	6	–	2	8	7	1
II	–	2	1	4	8	–	1	5	5	4
III	2	–	–	11	18	1	–	3	19	8
IV	–	–	1	13	–	1	–	2	10	1
V S.I. 7–12 feet[b]	–	4	6	24	6	–	2	4	11	23
" S.I. 25–30 feet	3	1	–	3	2	2	2	–	1	4
" S.I. 31–36 feet	–	1	–	–	4	2	–	–	–	3
" S.I. 37–42 feet	–	–	–	–	–	–	–	–	–	–
" S.I. 43–48 feet	2	5	–	–	1	2	3	2	–	1
Total	7	15	10	63	45	8	10	24	53	45
Percentage	*5%*	*11%*	*7%*	*45%*	*32%*	*6%*	*7%*	*17%*	*38%*	*32%*
	N. spathiger									
I	–	–	1	1	4	1	1	1	–	3
II	–	2	–	–	8	–	–	2	3	5
III	–	–	–	–	1	–	–	–	1	–
IV	–	–	–	–	5	–	–	–	2	–
V S.I. 7–12 feet	–	–	2	–	2	–	–	–	2	2
" S.I. 25–30 feet	1	2	1	13	10	–	2	5	13	2
" S.I. 31–36 feet	–	1	7	18	4	2	2	8	13	5
" S.I. 37–42 feet	1	–	–	11	1	–	1	5	7	3
" S.I. 43–48 feet	1	1	11	9	14	1	1	10	15	9
" Cecum[c]	1	2	4	10	9	–	2	2	13	9
Total	4	8	30	72	62	5	9	37	75	50
Percentage	*2%*	*5%*	*17%*	*41%*	*35%*	*3%*	*5%*	*21%*	*43%*	*28%*

[a] 0 : number of uteri not containing eggs.
[b] S.I. 7–12 feet, etc. : sections of small intestine measured from anterior end.
[c] *N. filicollis* not found in cecum.

TABLE 3.—*The relative frequency for* N. filicollis *and* N. spathiger *of egg segmentation stages in the lumen of the alimentary tract of sheep V at the time of autopsy*

Section of digestive tract	Number of eggs examined		Percentage of eggs in 1–4 cell stage		Percentage of eggs in 5–8 cell stage	
	N. fil.	*N. spath.*	*N. fil.*	*N. spath.*	*N. fil.*	*N. spath.*
S. intestine						
7–12 feet	94	23	68	61	32	39
19–24 "	112	28	54	54	46	46
31–36 "	36	141	53	50	47	50
43–48 "	135	247	37	32	63	68
Cecum	43	194	30	13	70	87

eggs segmented. Therefore while cleavages up to and including the third took place comparatively rapidly, the fourth was delayed for a time at least as long as it took for eggs to be transported from the anterior portion of the small intestine to the exterior in feces.

The Egg-laying Rate

In Table 1 it is shown that most worms contained an uninterrupted array of cleavage stages. This, it is concluded, indicates that the ovaries had been functioning just prior to sampling, if not continuously, then intermittently at short intervals.

Comparison of the number of eggs at each segmentation stage affords more precise information on the rate of egg production. Among those

TABLE 4.—*The mean frequency of the various segmentation stages of eggs in utero. This has been given also as a percentage of the mean frequency of unsegmented eggs*

Sheep	No. of worms averaged	Mean frequency of cell classes (*Percentages in parentheses*)							
		Anterior uterus				Posterior uterus			
		1	2	3–4	5–8	1	2	3–4	5–8
		N. filicollis							
I	18	11.1	2.7	1.8	1.1	19.4	4.0	0.8	0.2
		(100)	(24)	(17)	(10)	(100)	(21)	(4)	(1)
II	14	9.1	1.9	2.0	1.4	15.1	4.1	1.7	0.6
		(100)	(20)	(22)	(15)	(100)	(27)	(12)	(4)
III[a]	31	6.4	2.0	2.2	2.2	13.2	3.7	2.9	0.6
		(100)	(30)	(34)	(34)	(100)	(28)	(22)	(4)
IV	14	14.6	3.2	2.3	–	21.2	3.9	2.2	–
		(100)	(22)	(16)		(100)	(17)	(10)	
V S.I. 7–12 feet .	28	8.8	1.6	1.2	0.6	6.2	1.4	1.6	3.4
		(100)	(19)	(14)	(6)	(100)	(22)	(26)	(55)
		N. spathiger							
I	6	11.0	2.7	2.2	4.7	17.5	2.8	2.7	4.2
		(100)	(24)	(20)	(42)	(100)	(16)	(15)	(24)
II	10	7.4	2.2	2.3	4.7	14.1	4.9	2.3	2.3
		(100)	(30)	(31)	(64)	(100)	(35)	(16)	(16)
IV	4	9.2	2.2	2.2	6.5	15.5	3.5	4.0	1.2
		(100)	(24)	(24)	(70)	(100)	(23)	(26)	(8)
V S.I. 7–12 feet[b]	5	8.6	2.0	2.0	0.2	9.8	1.4	2.2	0.8
		(100)	(23)	(23)	(2)	(100)	(14)	(22)	(8)
" S.I. 37–42 feet	19	8.4	2.3	1.3	1.4	9.2	2.5	1.3	0.4
		(100)	(28)	(16)	(4)	(100)	(27)	(14)	(4)
" Cecum[c]	6	6.5	1.7	1.5	1.5	7.8	2.3	1.7	2.2
		(100)	(26)	(23)	(23)	(100)	(30)	(21)	(28)

[a] *N. spathiger* absent.
[b] S.I. 7–12 feet, etc.: section of small intestine measured from anterior end.
[c] *N. filicollis* not found in cecum.

worms in which there was an uninterrupted array of segmentation stages it was the rule in individual uteri for the mean number of eggs at particular cleavage stages, earlier than the maximal (i.e., the stage laid by the worm), to occur in a nearly constant ratio (Table 4).

In particular this applied to unsegmented and 2-cell eggs, the positive correlation between which is shown in Fig. 2. The individual fluctuation in the ratio is evident. It is concluded that, where the values for the ratio approached the mean, they were indicative of uniformity in the rate of

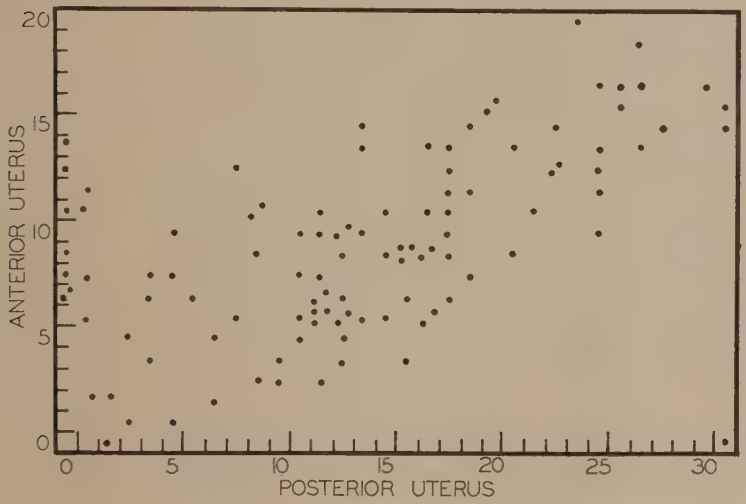

FIG. 1. The correlation in function between ovaries of the same individual of *Nematodirus filicollis*. The number of unsegmented eggs in one uterus, taken as an indication of this, has been plotted against the number in the other uterus of the same worm. In Table 4 the correlation between mean values for different sheep of each segmentation stage is given.

egg-laying on the part of individuals for at least a short time before sampling. A further conclusion is drawn that the differences between uteri in numbers, of a particular segmentation stage, indicated relative fecundity. For the reason that unsegmented eggs outnumbered 2-cell eggs the former are regarded as the more delicate index of this function. Obviously the sum of the numbers of unsegmented eggs for both uteri indicated the relative egg output for individual worms.

In Fig. 1, in which the numbers of unsegmented eggs of the anterior and the posterior uteri are plotted against one another, it is seen that there was positive correlation. Therefore, it follows that the uteri of worms did not alternate in function and that there was a direct relation in their relative fecundity. Table 5 shows that in sheep I, II, III, and IV the posterior ovary, by this same criterion of numbers of unsegmented

TABLE 5.—*The frequency with which one or other uterus contained the more unsegmented eggs*

Sheep	*N. filicollis*			*N. spathiger*		
	Number of worms	Frequency of uterine predominance in unsegmented egg numbers		Number of worms	Frequency of uterine predominance in unsegmented egg numbers	
		Anterior	Posterior		Anterior	Posterior
	(1)	(2)	(3)	(1)	(2)	(3)
I	18	1	17	6	–	6
II	14[a]	–	13	10	–	10
III	31	–	31	1	–	1
IV	14	1	13	4	–	4
V S.I. 7–12 feet ...	28[a]	19	6	5[a]	–	4
" S.I. 37–42 feet ...	–	–	–	19[a]	5	9
" Cecum	–	–	–	6[a]	1	4

[a] The difference between column (1) and the sum of columns (2) and (3) represents the number of worms in which the uteri contained equal numbers of unsegmented eggs.

eggs, produced eggs at a greater rate than the anterior ovary, and that in sheep V, the reverse took place. The direct relation between the two uteri in numbers of unsegmented eggs would mean that for particular conditions the worms functioned to the full extent of their potential.

The number of unsegmented eggs as an index of egg-laying rate is preferable to the total number of eggs found in worms. By the latter method no count is taken of the individual differences in capacity of the individual uteri, nor of time over which the eggs have been accumulated; the possibility of error is therefore greater.

A check on the use of the number of unsegmented eggs in estimating relative egg-laying rates, was obtained from results from the 7–12-foot section of the small intestine of sheep V. By totaling the number of unsegmented eggs of uteri, grouped according to the maximum stage of segmentation they contained, figures were obtained which it is considered indicated the proportional rate at which eggs of a particular stage of segmentation were being laid. Thus among worms of the sample population of *N. filicollis* which contained maximum stages of segmentation of less than four cells there was a total of 301 unsegmented eggs. Where the maximum degree of segmentation was of 5–8 cells, worms contained

TABLE 6.—*The frequency with which uteri contained unsegmented eggs*

Sheep	*N. filicollis*				*N. spathiger*			
	Number of worms	Uteri containing unsegmented eggs			Number of worms	Uteri containing unsegmented eggs		
		Anterior	Posterior	Per cent		Anterior	Posterior	Per cent
I	18	17	18	*97*	6	6	6	*100*
II	14	14	14	*100*	10	10	10	*100*
III	31	30	31	*98*	1	1	1	*100*
IV	14	14	13	*96*	4	4	4	*100*
V S.I. 7–12 feet[a] ..	28	28	22	*89*	5	5	5	*100*
" S.I. 37–42 feet ..	–	–	–	–	19	18	18	*95*
" Cecum	–	–	–	–	6	6	6	*100*

[a] S.I. 7–12 feet, etc.: section of small intestine measured from anterior end.

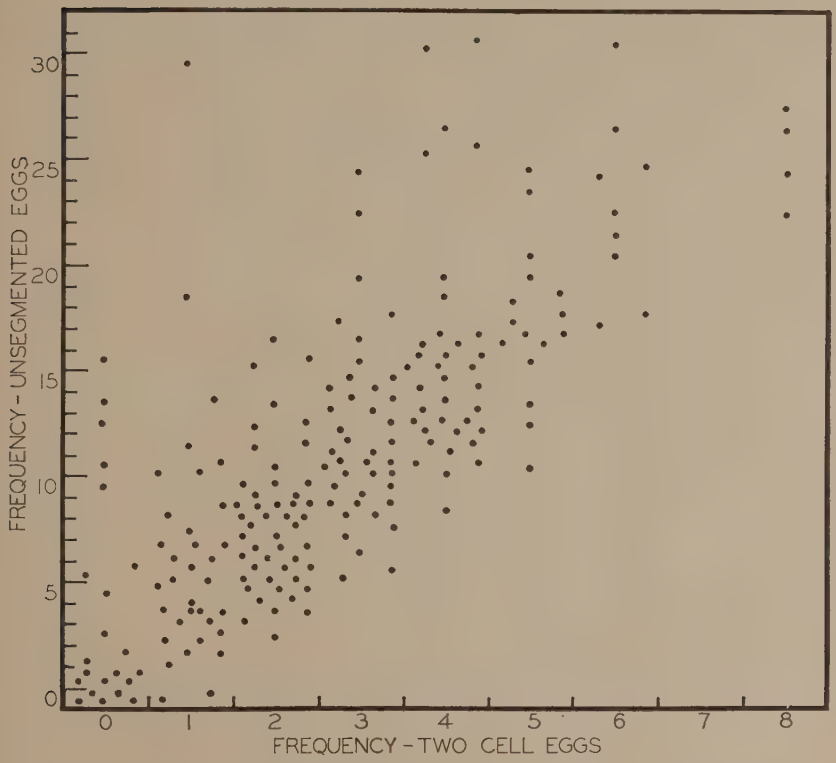

FIG. 2. The number of unsegmented eggs in each uterus of *Nematodirus filicollis* plotted against that of 2-cell eggs in the same uterus. The positive correlation shown is taken as an index of continuity in egg-laying by individuals. See Table 4 for the mean value, for each sheep, of the various segmentation stages.

a total of 100 unsegmented eggs. Comparison of this 3:1 ration was made with that of the same cleavage stages in eggs found free in the lumen of the intestine of this same region (Table 3). Here numbers were respectively 64 and 30, approximately a 2:1 ratio. In view of the small numbers involved and the lag in time between the laying and the examination of eggs found in the lumen the ratios are considered to approximate sufficiently to establish the validity of the numbers of the unsegmented eggs as a measure of the relative egg-laying rates of worms.

On reference to Table 6 it can be seen that among all five sheep the percentage number of uteri which contained unsegmented eggs ranged from 89 to 100 per cent for *N. filicollis,* and from 95 to 100 per cent for *N. spathiger.* These facts, coupled with the previously drawn conclusion that similarity of the ratios of numbers of unsegmented to 2-cell

eggs (Table 4) indicated continuity in egg-laying, lead to the additional conclusion that almost the entire population in each sheep was laying eggs at the time of sampling.

It is noteworthy that in sheep V, from which infection was in process of being eliminated, egg-laying was taking place, though at a retarded rate.

TABLE 7.—*The frequency of numbers of unsegmented eggs in utero in populations of* N. filicollis

Sheep	Class. Number of unsegmented eggs in utero	Frequency		
		Anterior uterus	Posterior uterus	Individual worms
I	0– 4	2	2	1
	5– 9	4	–	–
	10–14	7	3	1
	15–19	5	5	1
	20–24	–	2	2
	25–29	–	3	3
	30–34	–	3	3
	35–39	–	–	2
	40–44	–	–	2
	45–49	–	–	3
II	0– 4	2	2	1
	5– 9	5	–	–
	10–14	7	6	1
	15–19	–	2	2
	20–24	–	2	4
	25–29	–	2	1
	30–34	–	–	1
	35–39	–	–	4
III	0– 4	6	–	–
	5– 9	22	4	2
	10–14	3	14	4
	15–19	–	11	10
	20–24	–	2	7
	25–29	–	–	6
	30–34	–	–	2
IV	0– 4	1	1	–
	5– 9	–	–	–
	10–14	4	–	1
	15–19	8	3	–
	20–24	1	3	1
	25–29	–	6	1
	30–34	–	1	1
	35–39	–	–	5
	40–44	–	–	4
	45–49	–	–	1
V	0– 4	4	13	2
	5– 9	11	8	6
	10–14	12	4	8
	15–19	1	3	3
	20–24	–	–	5
	25–29	–	–	3
	30–34	–	–	1
	35–39	–	–	–
	40–44	–	–	–

The inter-host differences in magnitude of the mean number of uterine unsegmented eggs per individual (Table 4) and the tendency in a population of worms from one host for the uterine number of unsegmented eggs to fluctuate according to the curve of error (Table 1), suggest that the mean value is an index of the particular set of conditions in which the populations were found. It would follow as a corollary that fecal egg numbers also are a measure of these conditions. A further corollary

would be that periodical fluctuations in the fecal egg count have significance in this connection.

In the estimation of the absolute mean fecundity, from fecal counts and the numbers of females found at autopsy, the foregoing indicate that the mean values refer to the modal rate of egg production of the worm population at a particular point of time. Variance in the mean values found for a species, it is concluded, reflects not variance in the numbers of worms which have contributed to the population of eggs, but rather in the particular level for the whole population of the tide of egg production at that time.

SUMMARY

A study was made of degree of segmentation and numbers of in utero eggs of *N. filicollis* and *N. spathiger*. It is concluded that:

1. At any one point of time almost the entire population of worms is laying eggs.

2. The numbers of unsegmented eggs in utero indicate the relative fecundity of worms.

3. Among a population of worms the individual fecundity fluctuates about a mean according to the normal curve of error.

4. The absolute mean rate of egg production for individual worms as determined from fecal egg numbers and the population of females found at autopsy, refers to the modal rate of egg production at a particular level in the fluctuating tide of egg production.

5. Fecal egg numbers are an index of the relative behavior of the population as a whole to a particular set of conditions at one point or over a short period of time.

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EARLY DEVELOPMENTAL STAGES OF STRIGEID TREMATODES IN THE FIRST INTERMEDIATE HOST*

W. W. Cort and Louis Olivier

HISTORICAL INTRODUCTION

Although the life cycles of more than twenty species of strigeids have been worked out more or less completely, very little is known of the germ cell cycle in this group or of the early stages of development in the first intermediate host. We have found only three studies of strigeid miracidia which give information on the germ cells. Van Haitsma (1930) considered as primordial germ cells a small but variable number of large granular cells which he found in the posterior end of the miracidium of *Diplostomum flexicaudum* (Cort and Brooks, 1928). In one of his figures (Pl. XLV, Fig. 24) he showed four such cells in a row, and labelled them "germ cells." Hunter and Hunter (1935, Pl. C, Fig. 1) depicted a single "germ ball" in the posterior end of the miracidium of *Crassiphiala* (= *Uvulifer*) *ambloplitis* (Hughes, 1927). Park (1936) observed a "germ cell sac" near the posterior end of the miracidium of *Neodiplostomum lucidum* La Rue and Bosma, 1927, which contained a coarse granular fluid and from one to several large floating germ cells. He also regarded as germ cells other large cells lying in the parenchyma anterior to the "germ cell sac."

Looss (1896) seems to have been the first to see a strigeid mother sporocyst. He described and figured (Pl. XV, Fig. 162) this stage of *Cercaria vivax* Sonsino, 1892, which was later shown by Azim (1932) to develop into an adult of the strigeid family Cyathocotylidae. Looss also made some very interesting observations on daughter sporocysts of this species. In the youngest daughter sporocysts outside the mother, which were only about 0.3 mm in length, he found two types of germinal elements ("corps germinatifs") free in the body cavity. Some of them were evidently cercarial embryos. The others were irregular structures divided into three or four distinct segments each composed of groups of cells. Looss suggested that these segments probably separated to form cercarial embryos. In the figures of an older sporocyst in which cercariae were beginning to be differentiated he also showed several of these compound structures (Pl. XV, Fig. 165).

Sewell (1922, p. 284) reported the finding of mother sporocysts of *Cercaria indicae* XV, a form closely related to *C. vivax*. The largest were almost 10 mm in length and had a terminal birth pore.

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Mathias (1925) exposed snails to large numbers of the miracidia of *Strigea tarda* [= *Cotylurus cornutus* (Rud.)] and examined them at intervals to follow early development. In this way he obtained early stages of mother sporocysts, which showed the metamorphosis from the miracidia (Pl. II, Fig. 9 a, b, c). He probably had multiple infections since he exposed the snails to large numbers of miracidia. He concluded that the sporocyst that metamorphosed from the miracidium ("sporocyste primitif") produced a number of new sporocysts ("sporocystes primaires") by transverse fission. The latter then invaded the tissues of the snail and gave rise to another generation of sporocysts ("sporocystes secondaires") which in turn produced the cercariae. Mathias believed that mother sporocysts reproduced by transverse fission because they were often divided into segments by constrictions in the wall (Fig. 9 d).

Brooks (1930) included four species of strigeids in the material used in his study of the germ cell cycle of digenetic trematodes. From the examination of sections of young daughter sporocysts he concluded that the germ cells ("antecedent germ cells") lie free in the body cavity. According to his view these "antecedent germ cells" form "germ masses," which are rather loosely associated groups of undifferentiated cells. These masses later separate into their individual cells ("excomponents") each of which produces a cercarial embryo. He interpreted this method of reproduction as a "specific polyembryony or blastotomy."

Wesenberg-Lund (1934) found the mother sporocysts of five different species of strigeids in examinations of naturally infected snails. They were present along with fully developed daughter sporocysts containing mature cercariae and were all old and almost empty. He recognized them as mother sporocysts from their large size and because they contained a few small daughter sporocysts. They varied considerably in length in the different species and some of them were divided into sections by constrictions.

Hunter and Hunter (1935) found structures which they interpreted as mother sporocysts in snails naturally infected with *U. ambloplitis*. These structures were only 0.2 to 0.3 mm in length and had definite eyespots.

MATERIALS AND METHODS

Most of the studies reported in this paper were made on strigeid infections found in juveniles and adults of *Stagnicola emarginata angulata* (Sowerby) collected in the Douglas Lake region during the summer of 1940. In the examination for infections the bodies of the snails were carefully removed from the shells and observed with a low power binocular microscope. If no sporocysts were seen on the surfaces of the organs, we then teased the tissues apart with dissecting needles, looking most carefully in the region between the digestive gland and the foot. When

a mother sporocyst was found, we tried to remove it unbroken for measurement and study while still alive. Daughter sporocysts were studied in the same way. Several *intra vitam* stains, particularly neutral red, were tried but in most cases the details could be worked out best from unstained specimens mounted in normal saline.

Some of the infections, although obviously strigeids, could not be specifically identified because of their immaturity. In other cases, however, we were able to study mother sporocysts and young daughter sporocysts from infections in which some of the cercariae were mature enough for identification.

DATA FROM THE OBSERVATIONS

Mother sporocysts: A total of 21 strigeid mother sporocysts from naturally infected juveniles and adults of *S. emarginata angulata* were studied during the summer of 1930. Ten were in infections too immature for identification; six belonged to *Diplostomum flexicaudum* (Cort and Brooks, 1928); two to *Cercaria laruei* Cort and Brooks, 1928; two to *C. emarginatae* Cort, 1917; and one to *C. dohema* Cort and Brackett, 1937. In addition, a mother sporocyst was recovered on November 5, 1940 from a laboratory raised juvenile of *S. emarginata angulata* which had been exposed 25 days before to miracidia of *Diplostomum micradenum* (Cort and Brackett, 1938). All these mother sporocysts with the exception of one found on the surface of the basal portion of the digestive gland, were laced in among the organs and ducts between the foot and digestive gland. Frequently a portion of the sporocyst projected from the surface of the undissected snail body, but many of them were found only after careful dissection of the tissues under the mantle on the upper side of the foot.

Almost all the mother sporocysts observed had already given off most of their daughter sporocyst progeny. They were sometimes found in infections in which there were mature cercariae. In such cases, the infection would also contain a whole series of immature daughter sporocysts in the various stages of development. A few of the mother sporocysts, however, still contained all or most of their daughter sporocyst brood. When in position in the host all but a few of the very oldest mother sporocysts appeared as inflated sacs of uniform diameter. When freed intact in normal saline they moved actively; but when they were removed to slides for microscopical examination they were easily broken and frequently sections would collapse. Strigeid mother sporocysts have thick walls consisting of a thin cuticula, muscular layers and a single layer of cells bordering on the large body cavity. The anterior end is attenuated and has a terminal birth pore (Figs. 1, 2).

Most of the mother sporocysts were considerably larger than the daughter sporocysts, especially in width. Four, from infections too im-

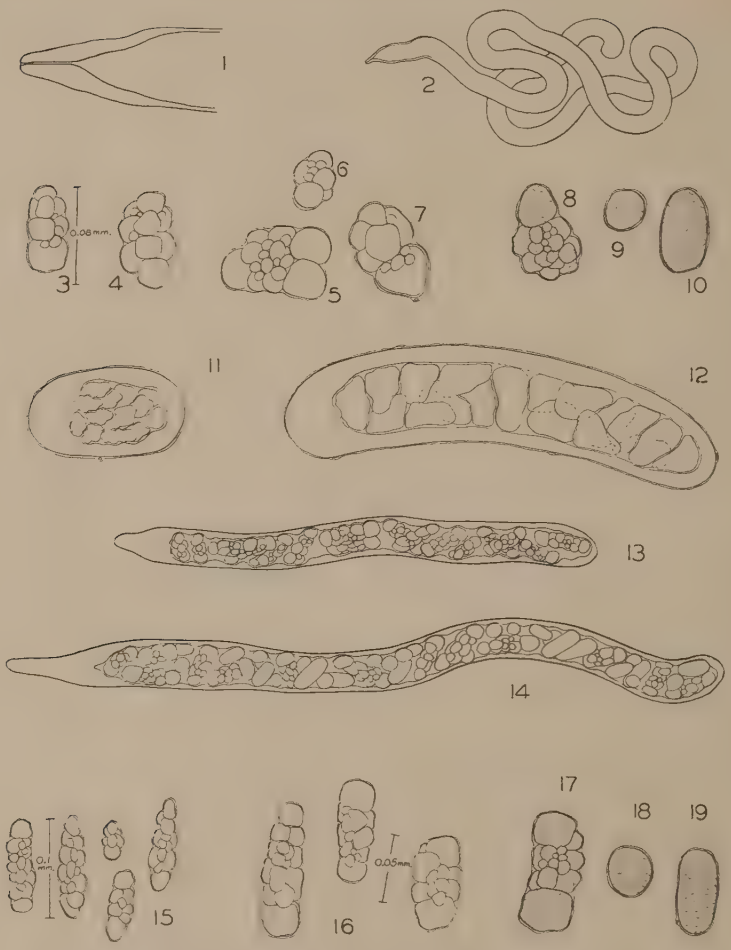

Fig. 1. Anterior end of mother sporocyst of *D. flexicaudum* showing birth pore.

Fig. 2. Complete mother sporocyst of *D. flexicaudum*.

Figs. 3–7. Outline drawings of germ masses from strigeid mother sporocysts. All drawn to same scale.

Fig. 8. Germ mass from mother sporocyst showing large and small multicellular components and also single-celled components.

Fig. 9. Very young daughter sporocyst embryo (a germ ball). Note similarity to largest component of germ mass (Fig. 8).

Fig. 10. Older daughter sporocyst embryo drawn to same scale as Fig. 9, showing elongation.

Fig. 11. Daughter sporocyst embryo, 0.075 mm long. Note germ masses in body cavity, each composed of several cells.

Fig. 12. An older daughter sporocyst embryo, 0.2 mm long. Note germ masses in body cavity which already have many celled components.

mature for identification, were 5, 7, 10, and 12 mm long. Those of *D. flexicaudum* measured up to 10 mm in length and varied from 0.13 to 0.32 mm in diameter. Two of *C. laruei* measured 17 and 25 mm in length and one of *C. emarginatae* was about 8 mm long and 0.3 mm wide. Except for the larger size in *C. laruei* no specific differences were observed among the mother sporocysts of the five species. Differences, however, will probably be found when more material becomes available for comparative study. Mother sporocysts live and continue to reproduce for a considerable period of time (at least five or six weeks and probably longer) since they were frequently found in infections from which large numbers of cercariae were escaping.

Contents of mother sporocysts: In most of the mother sporocysts elongate slender daughter sporocysts were found which appeared to be about ready to emerge. There were also present the various developmental stages of the daughter sporocysts, and a few peculiar structures, which could be easily distinguished from the daughter sporocyst embryos by their irregular outline. They will be referred to as germ masses, using the term employed by Brooks (1930) for similar structures in daughter sporocysts.

Germ masses: The germ masses found inside the mother sporocysts were few in number. They varied in length from about 0.05 to 0.12 mm and were composed of a variable number of components all enclosed by a thin membrane (Figs. 3–7). The largest components which were usually at the ends were composed of a mass of cells and were completely surrounded by their own membrane. In a few cases the large end components were seen partly split off from the rest of the germ mass. The germ masses also contained smaller components composed of cell groups and a few distinctly separated single cells near the middle of the mass (Fig. 8).

Daughter sporocyst embryos: The youngest daughter sporocyst embryos (Fig. 9) were small spherical structures about 0.025 mm in diameter composed of a number of cells and enclosed by a thin membrane in which flattened nuclei could sometimes be distinguished. They were

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Fig. 13. Daughter sporocyst (embryo) 0.8 mm long from mother sporocyst. Note that only germ masses are present in the body cavity.

Fig. 14. Daughter sporocyst dissected from snail tissue and evidently recently emerged from the mother. Note many germ masses but also a number of very young cercarial embryos.

Fig. 15. Outline drawings of germ masses from daughter sporocysts before they emerged from the mother. Drawn to same scale.

Fig. 16. Outline drawings of germ masses from young daughter sporocysts dissected from snail tissue.

Fig. 17. Germ mass from daughter sporocyst showing large and small multicellular components and also single celled components.

Fig. 18. Very young cercarial embryo. Note similarity to larger components of germ mass (Fig. 17).

Fig. 19. Cercarial embryo slightly older than in Fig. 18.

about the same size and had exactly the same structure as the largest components of the germ masses. A daughter sporocyst embryo in slightly later stage, which was more elongate but in which no differentiation of the cells could yet be distinguished, is shown in Fig. 10. In daughter sporocyst embryos about 0.05 mm long the body wall could be first seen as separate from the germinal material in the cavity; and at a somewhat later stage, about 0.07 to 0.08 mm long, the wall was very clearly separated from the contents of the body cavity (Fig. 11). The body wall in these early daughter sporocyst embryos was comparatively thick and consisted mainly of the single layer of large cells lining the cavity. The germinal material at this stage was organized into a number of germ masses, the components of which appeared to be single cells. An older stage (Fig. 12), about 0.2 mm in length, contained germ masses in which some of the components already consisted of cell groups. Still older daughter sporocyst embryos were studied in a 25-day-old mother sporocyst of *D. micradenum* which developed from an experimental infection. About 20 daughter sporocysts were observed in this mother, none of which appeared to be ready to escape. Seven that were measured varied from 0.31 to 0.46 mm in length and from 0.03 to 0.05 mm in width. The numbers of germ masses they contained could be easily counted and varied from 12 to 19.

Daughter sporocyts ready to emerge from the mother (Fig. 13): Daughter sporocysts which appeared to be about ready to emerge from the mother were quite mobile and had a considerable power of extension and contraction. They varied in length from about 0.6 to 1.0 mm and were sometimes as much as 0.1 mm in diameter. The anterior end of the daughter sporocysts at this stage was attenuated and very mobile and the body cavity did not extend into it. No trace of the birth pore could be seen. A careful examination disclosed that the body wall was composed of a thin outer cuticula, muscular layers, and a single layer of cells bordering on the body cavity. In the body cavity were a number of germ masses which did not fill the cavity and which moved back and forth in it with the movement of the sporocyst. Sometimes the germ masses were crowded into less than half the length of the cavity. The number of germ masses in a series of 18 of these daughter sporocysts varied from 13 to 23 with an average of 17. The material examined was not sufficient to determine whether the number of germ masses varies with the species. These germ masses varied in length from 0.02 mm to almost 0.12 mm. While essentially like those found in the mother sporocysts, they were generally somewhat smaller and tended to be more elongate. They had a variable number of components, the typical arrangement of which is shown in Fig. 15. Single cells were never found in the body cavity of daughter sporocysts. In only three cases were early cercarial embryos seen in daughter sporocysts still within the

mother. One of these was a daughter sporocyst of *D. flexicaudum,* 0.8 mm in length, which contained, in addition to 20 germ masses, four cercarial embryos. Also, in two daughter sporocysts of *C. emarginatae* which were still within the mother there were two and six of these very young cercarial embryos. These findings and the constant presence of cercarial embryos in the youngest daughter sporocysts found outside the mothers, indicate that the first cercarial embryos are just beginning to appear at the time of emergence of the daughters from the mother.

Daughter sporocysts from host's tissues: In young infections the immature daughter sporocysts may all be located among the organs in front of the digestive gland; some, however, always reach this gland rather early in the development of the infection. In older infections in which some cercariae have reached full development, the daughter sporocysts will have invaded almost the whole of the digestive gland, but numbers of them remain between the foot and this gland. In a number of cases the mother sporocysts still contained a few daughters after the infection had reached maturity. In such infections a whole series of the different developing stages of daughter sporocysts would be found in the snail's tissues, including some about the same size as those still contained in the mother.

Most of the youngest daughter sporocysts outside the mothers showed an increase in size (Fig. 14). In their body cavities mixed in with the germ masses were varying numbers of the youngest cercarial embryos (Fig. 18). They were very much like the youngest daughter sporocyst embryos and were also about the same size and of exactly the same structure as the largest end components of the germ masses (cf. Figs. 17 and 18). Each consisted of a spherical mass of apparently undifferentiated cells surrounded by a thin membrane containing a few flattened nuclei. These youngest cercarial embryos increased considerably in size while still appearing as a mass of cells (Fig. 19). Soon the individual cells could not be seen and the size increased further. Later the differentiation of body and tail occurred. As the daughter sporocysts increased in size, the number of developing cercarial embryos rapidly increased but the number of germ masses apparently remained constant.

A series of counts of the germ masses and cercarial embryos was attempted in young daughter sporocysts of different sizes dissected from the tissues of the snails. One unidentified daughter sporocyst 1.3 mm in length contained 18 germ masses and 24 cercarial embryos, the largest of which was only about 0.06 mm long as compared with 0.12 mm for the largest germ mass. In a sporocyst of *C. laruei,* 1.34 mm in length, there were 18 germ masses and about 40 cercarial embryos some of which showed considerable differentiation; and in a sporocyst of *C. emarginatae* of about the same size there were 17 germ masses and 25 very young cercarial embryos. The contents of three unidentified daughter sporocysts

1.8 to 2.0 mm in length were also counted. They contained 20, 26, and 16 germ masses respectively and about 50, 93, and 100 cercarial embryos, the oldest of which had not yet reached the stage of tail differentiation. In a few larger sporocysts up to over 4 mm in length counts were made which gave the impression that even at the stage where the cercariae show a well differentiated body and tail there was no reduction in the number of germ masses. Fig. 16 shows germ masses from the young daughter sporocysts after their escape from the mother.

In a considerable number of mature and old daughter sporocysts of *D. flexicaudum, C. laruei, C. emarginatae,* and *C. yogena* Cort and Brackett, 1937, from 2 to 10 germs masses were still found, scattered among cercarial embryos in all stages of development. We could not be certain that there was really a reduction in the numbers of germ masses in such sporocysts because the numerous cercarial embryos tended to obscure them. Germ masses and immature cercarial embryos were even found in sporocysts so old that they were almost entirely empty. The germ masses found in mature and old sporocysts differed little from those in the immature sporocysts. In 12 such germ masses the number of multicellular components varied from 4 to 9 and the single celled components from 2 to 5. We have gained the general impression from these observations that there are fewer germ masses in the oldest sporocysts and that those that are left have somewhat fewer components. The most significant point, however, is that even in old sporocysts, which are partly empty and beginning to degenerate, germ masses and very immature cercarial embryos may still be found.

Numbers involved in development: We obtained a little information on the number of daughter sporocysts and cercariae normally produced from a single miracidium. In one case more than 50 daughter sporocysts in addition to some germ masses and developing embryos were found inside a mother sporocyst; and in another case over 60 daughter sporocysts were dissected from the tissues of a juvenile snail. Although it will have to be checked by later studies, we have the general impression that the number of daughter sporocysts produced by a single mother may be considerably larger. Finally, in one daughter sporocyst 8.7 mm in length in which none of the cercariae were mature we counted almost 1,000 embryos.

DISCUSSION

The data from our investigations given above make it possible to understand more clearly some of the phases in the life cycle of the strigeids. On the basis of the descriptions of Van Haitsma (1930), Hunter and Hunter (1935), and Park (1936) it appears that strigeid miracidia contain only a small number of germ cells. It is suggested that each of these germ cells develops into a germ mass when the miracidium metamorphoses into the mother sporocyst. Our observations indicate to us

that these germ masses give rise to the daughter sporocyst embryos by splitting off their larger components and are the only source of daughter sporocyst embryos. The striking similarity between the youngest daughter sporocyst embryos and the largest of the germ mass components supports that view. Also, the germ masses are loosely organized and in many cases the largest components appear to be ready to split off or are even occasionally partly separated from the rest of the mass. Evidently daughter sporocyst embryos begin to split off from the germ masses rather early in the development of the mother sporocysts. This would account for the production of the first mature cercariae in about six weeks after the penetration of the miracidium into the snail (Van Haitsma, 1930; Mathias, 1925). New daughter sporocyst embryos are split off over a considerable period of time, probably a month or even more. The evidence for this is that mother sporocysts which were obviously old and which had produced daughters which were already mature contained germ masses and young daughter sporocyst embryos. To make possible this long period of production of daughter sporocysts it is evident that the cells of the germ masses must continue to divide and to produce new components as the largest ones break off.

We did not find the slightest evidence in our studies that mother sporocysts reproduce by fission or fragmentation as suggested by Mathias (1925).

Our studies also suggest that very early in the development of the daughter sporocyst embryo a small number of cells of the germinal line come to lie in the cavity surrounded by the soma and that each of these develops into a germ mass. We believe that these germ masses of the daughter sporocysts are the only source of cercarial embryos and give rise to them by the splitting off of the largest components. There is considerable evidence for this view. In the first place, germ masses are the only structures we have seen in the body cavities of the developing daughter sporocysts up until about the time that they emerge from the mother; we have constantly looked for single germ cells but have never found them. Also, the youngest cercarial embryos are strikingly like the largest end components of the germ masses. Finally, it has been observed that the largest components may be loosely attached to and even partly separated from the rest of the germ mass and appear to be ready to break off.

As suggested for the germ masses of the mother sporocysts, the single cell elements of the germ masses of the daughters must continue to divide and produce new multicellular components to take the place of those that are split off. The best evidence that such division does occur comes from the fact that the germ masses of old daughter sporocysts in which large numbers of cercariae have been produced still have single-celled components. Also, the total number of components in the germ masses

found in a young daughter sporocyst is much smaller than the number of cercariae usually produced by each daughter.

The most significant contribution made in this study is the description of the germ masses of the mother and daughter sporocysts and the elucidation of the method of production of the daughter sporocyst and cercarial embryos. It is not at all surprising that germ masses have not been recognized previously in mother sporocysts since so little attention has been paid to this phase of the strigeid life cycle. Perhaps the single "germ ball" that Hunter and Hunter (1935, Pl. C, Fig. 3) figured in the posterior end of the mother sporocyst of *U. ambloplitis,* and the groups of cells shown by Mathias (1925, Pl. II, Fig. 9) in the end segment of a mother sporocyst of *C. cornutus* were really germ masses.

On the other hand, the germ masses of the young daughter sporocysts of strigeids are such conspicuous and unusual structures and so different from all the stages of the cercarial embryos, that it is surprising that they have not been observed more often. As noted above Looss (1896) described what appear to be germ masses in his studies of young sporocysts of *C. vivax*. He even suggested that cercarial embryos were produced by the separation of the multicellular components of these structures. Also, the "germ balls" figured by Mathias (1925, Pl. III, Fig. 4) in the body cavity of a young sporocyst were undoubtedly germ masses.

Brooks (1930) came the closest to a correct interpretation of the part played by the germ masses in strigeid development. He interpreted them as masses of cells formed by the division of the original germ cells ("antecedent germ cells"). According to his view the cercarial embryos were formed by the breaking up of these masses into single-celled "excomponents" each of which formed a cercarial embryo. He described and figured single cells, which he interpreted either as "antecedent germ cells" or "excomponents" in the body cavities of young strigeid daughter sporocysts. We have found only germ masses or cercarial embryos, never single cells, in the body cavities of the young living daughter sporocysts we have observed. This difference in observations was not due to the use of different material, since two of the species Brooks studied, *C. laruei* and the cercaria of *D. flexicaudum,* were also studied by us. It may be significant in this connection to note that when daughter sporocysts were kept too long in normal saline, the youngest cercarial embryos tended to disintegrate, freeing numbers of single cells. Since Brooks made all his studies on fixed and sectioned material, it may be that some of the embryos or germ masses disintegrated during fixation or manipulation. It is also significant that the two strigeid germ masses which Brooks figured (Pl. III, Figs. 40 and 42) clearly show many-celled components and that he suggested that these components were the early stages of cercarial embryos, which had precociously developed before the single-celled components were separated from the germ mass.

Most of the recent studies of the germ cell cycle of digenetic trematodes support the theory of "germinal lineage" (Dollfus, 1919; Brooks, 1930; Cable, 1934; and Chen, 1937). According to this view reproduction in the first intermediate host is brought about by the segregation of germ cells, which early in embryonic development come to lie in the body cavities of the sporocysts or rediae. These germ cells multiply and eventually give rise to numerous progeny apparently without undergoing maturation or fertilization. Our work on the early developmental stages of the strigeids fits in with this view. In this group, however, a great multiplication of individuals is brought about by the development from the germ cells of a limited number of discrete structures, the germ masses, which produce numerous progeny over a considerable period of time. This development of daughter sporocyst and cercarial embryos by the splitting off of components from the germ masses may perhaps be considered as a special type of polyembryony.

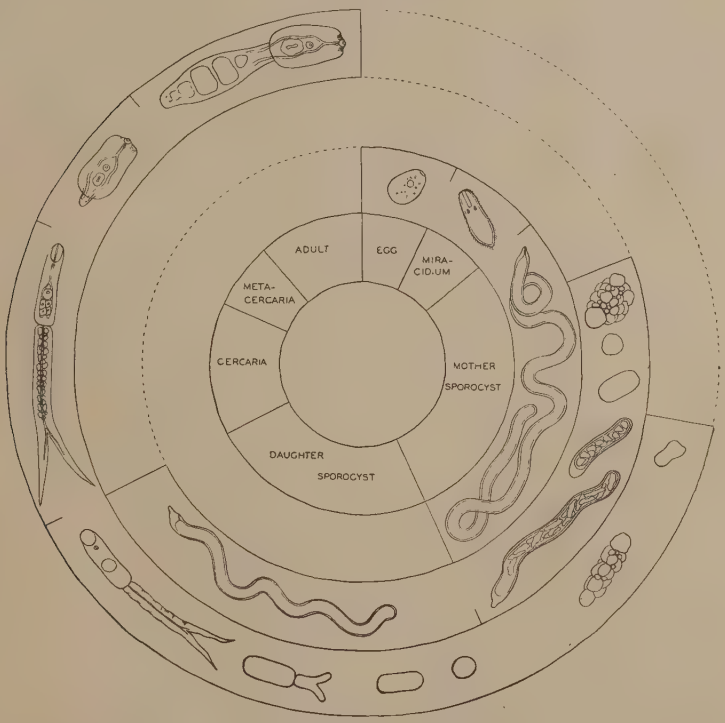

FIG. 20. Diagrammatic outline of the life cycle of a strigeid, *Diplostomum flexicaudum*.

SUMMARY OF THE LIFE CYCLE IN THE STRIGEIDS

From the evidence given in the preceding discussion, the life cycle in the strigeid group may be considered as a succession of three generations in two of which there are phases of reproduction by a special type of polyembryony (see Fig. 20). The first generation begins with the fertilized ovum produced by the adult, includes the free living miracidium, and ends with the mother sporocyst parasitic in the first intermediate host. The second generation begins with the few germ cells set aside in the development of the miracidium which produce the germ masses found in the mother sporocyst. These germ masses give rise to the daughter sporocysts which leave the mother sporocyst to finish their development in the tissues of the first intermediate host. The third generation starts with a small number of germ cells separated from the soma early in the development of the daughter sporocyst embryo. These produce germ masses, the end components of which begin to be freed as cercarial embryos at about the time the young daughter sporocysts escape from the mother. New cercarial embryos continue to be formed in the same way during the whole life of the daughter sporocysts. The cercariae escape from the snail host and penetrate into a second intermediate host where they go through a long period of metamorphosis to produce the fully developed metacercariae. These, after transfer to the definitive host, develop in a comparatively short time into adults.

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A REDESCRIPTION OF *CONTRACAECUM MULTIPAPILLATUM* (VON DRASCHE, 1882) (NEMATODA: ANISAKINAE)

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In this paper the writer presents a redescription of *Contracaecum multipapillatum* because it is evident from the literature (1) that the species concept of von Drasche (1882) needs more detailed and complete definition and (2) that the description by Skrjabin (1916) of an entirely different species as identical with *Ascaris multipapillata* has resulted in confusion as to the morphological characteristics of von Drasche's species.

The specimens which the writer regards as identical with *A. multipapillata* von Drasche, 1882 and upon which this redescription is based were examined in connection with a study of representatives of the subfamily ANISAKINAE in the Helminthological Collection of the U. S. National Museum.

In addition to the following review of the literature and redescription of von Drasche's species, this paper includes a proposal of a new name for the specimens which the writer regards as misidentified by Skrjabin.

REVIEW AND CRITIQUE OF THE LITERATURE

Von Drasche's (1882) description of *Ascaris multipapillata* included no statements as to the nature of the digestive tract and was incomplete in several other respects, but was sufficient to permit recognition of the species. Stossich (1896) mentioned the species but added nothing concerning its morphology. As has been noted, Skrjabin (1916) published a detailed description of *"Contracoecum multipapillosa* (Drasche 1882)". Obviously, Skrjabin considered that he had redescribed *Ascaris multipapillata* and had allocated the species, on the basis of the structure of the specimens before him, to the genus *Contracaecum* Railliet and Henry, 1912. However, in the specimens from *Ardea* sp. described by Skrjabin, interlabia were absent, whereas von Drasche described and figured interlabia in *Ascaris multipapillata.* Skrjabin stated that 10 pairs of postanal papillae were present in his specimens, 7 pairs being lateral in position and 3 pairs submedian. He did not mention the presence of double papillae. His illustration of the lateral aspect of the male tail (Pl. 24; Fig. 8), according to the legend pertaining to it, indicated the presence of 7 pairs of lateral postanal papillae; evidently, the submedian papillae were intentionally omitted from the figure. Von

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Drasche (1882) stated that 10 postanal papillae (obviously from his figure, 10 pairs) are present in the male of *A. multipapillata;* he noted that papillae 5–10 are arranged in two rows behind the anus and that papillae 5 and 6 may be regarded as a double papilla. In one specimen, von Drasche found a third papilla united with these two on one side of the tail. His figure showed that 2 of the 4 pairs of papillae in the subterminal group were lateral or sublateral in position; possibly, 2 pairs of the single papillae just behind the cloaca might be considered sublaterals, but their position ordinarily would be regarded as subventral. Hence von Drasche figured 8 pairs of subventral and 2 pairs of lateral postanal papillae in *A. multipapillata.* This arrangement differs markedly from that described by Skrjabin.

It should be noted that Skrjabin's illustration (Pl. 24; Fig. 8), contrary to his statements in the legend and text, appears to show that the 7 postanal papillae figured actually were subventral rather than lateral in position. However, since the remaining 3 of the 10 postanal papillae reported to be present were not figured, the only existing evidence as to their position is Skrjabin's statement that it was submedian. Therefore, it cannot be shown on the basis of any justifiable interpretation of the data given by Skrjabin that the postanal papillary pattern of his specimens was identical with or closely resembled that figured for *A. multipapillata* by von Drasche. Finally, the fact that Skrjabin's specimens were reported to lack interlabia leaves no alternative but to conclude that they were of a species distinct from von Drasche's. Although Skrjabin, therefore, did not clarify the structure, or establish the systematic position of *A. multipapillata,* he could have been credited with the transfer of the species to *Contracaecum* had his spelling of the specific name corresponded to that of von Drasche.

In the same year, Gedoelst (1916) assigned "*Ascaris multipapillata* Drasche 1882" to *Kathleena* Leiper and Atkinson, 1914, without, however, combining *Kathleena* and *multipapillata.* Baylis (1920) synonymized *Kathleena* with *Contracaecum,* and tentatively included in *Contracaecum* all of the species referred to *Kathleena* by Gedoelst; he also made the combination "*Contracaecum multipapillatum* (v. Drasche, 1882)". As has been previously stated, von Drasche did not describe the digestive tract of *Ascaris multipapillata* and, so far as is evident from their papers, neither Gedoelst nor Baylis had any knowledge concerning its structure. Actually it is of the *Contracaecum* type. Thus, Baylis (1920) receives credit for the transfer of von Drasche's species to *Contracaecum* for he first made the proper combination.

Later writers have referred to *C. multipapillatum,* but have contributed no information as to its morphology with one probable exception. Walton (1923) mentioned the species in discussion and Layman

and Mudretsova (1926) included "*C. multipapillata*" in their key to species of the genus. It is evident from this key that the Russian authors had in mind the specimens described by Skrjabin (1916), not *C. multipapillatum* (von Drasche). Cram gave an account of the morphology of "*Contracaecum multipapillatum* (Drasche, 1882) Baylis, 1920b"; it combined data and illustrations taken from both von Drasche and Skrjabin and, therefore, must be regarded as actually relating to two species. Witenberg (1929) mentioned "*C. multipapillosum* (Drasche)", but apparently his remarks were based on Cram's account. Hsü (1933) described the esophageal glands of "*Contracaecum multipapillatum* (Drasche, 1882)". While Hsü's paper contained no reference to specific characters, there is no reason to question his identification and it may be presumed that his work first established that the *Contracaecum*-type esophagus occurs in von Drasche's species. So far as the writer has been able to determine, there have been no other referencs to *C. multipapillatum*.

Contracaecum multipapillatum (von Drasche, 1882) Baylis, 1920

Synonymy: Ascaris multipapillata von Drasche, 1882; *A. multipapillosa* Skrjabin, 1916 [=*A. multipapillosa* Drasche 1882 of Skrjabin (1916)]; nec *Contracaecum multipapillosa* Skrjabin, 1916 [=*Contracoecum multipapillosa* (Drasche 1882) of Skrjabin (1916)].

Description: In median optical section of body, edges of cuticular striae in region just behind lips serrated (Figs. 1, 2, 3); diameter of head less than diameter of body just behind lips. Lips widest near anterior extremities and narrowest at base; height and greatest breadth about equal. Anterior margin of pulp only slightly indented medially and antero-lateral margins more or less rounded when outer surface of lip is viewed (Fig. 3); cuticle extending beyond pulp anteriorly and inwardly toward axis of mouth, medially indented forming two lobes (Figs. 3, 5); cuticle also extending beyond pulp in antero-lateral regions forming more or less triangular wing-like projections (Figs. 3, 5). From angle of greatest lateral expansion outline of cuticular projections passing toward median line intersecting pulp near location of cephalic papillae then curving posteriorly concavely to origin (Fig. 3). Pulp indented just behind location of papillae; outline then curving convexly to posterior origin. Internal, principally cuticular, portion of lip narrowest where pulp is widest (Fig. 3). In en face view of lips, pulp divided into an external and internal section near base of lips; external section extending farther anteriorly than internal section, but neither extending into anterior internal lobes of lip or extremes of antero-lateral projections (Fig. 5). When lip is viewed from outer surface, the pulp forms two lateral lobular areas of greatest density which are widest in region beneath papillae and taper posteriorly. Interlabia robust in median longitudinal section (Fig. 3), nearly as high as lips; broad at base, curving inward toward mouth axis, tapering anteriorly to rounded tip; roughly triangular in outline when viewed from external surface (Fig. 1). Muscular esophagus long and slender; diameter almost uniform. Esophageal ventriculus small, oval, width greater than length. Esophageal appendix short, slender, typically 1/7 to 1/8 as long as esophagus. Intestinal cecum extending almost to position of nerve ring; voluminous at origin, tapering to an anterior tip about equal in diameter to esophagus. Cecum roughly 4/5 as long as esophagus (Fig. 2). Lateral cervical papillae sessile, near level of nerve ring.

The principal size relationships of 2 female and 5 male specimens are shown in Table 1.

TABLE 1.—*Principal size relationships of* Contracaecum multipapillatum.
(*All measurements in mm.*)

	Females		Males				
	1	2	1	2	3	4	5
Body							
Length	35.0	35.0	25.0	18.0	16.0	18.5	12.7
Maximum width	1.09	1.0	0.79	0.77	0.83	0.62	0.54
Muscular esophagus							
Length	4.98	4.76	3.84	3.69	3.47	2.80	2.58
Average width	0.15	0.15	0.14	0.14	0.17	0.12	0.10
Esophageal ventriculus							
Length	0.14	0.14	0.12	0.08	0.10	0.08	0.06
Width	0.19	0.21	0.17	0.16	0.17	0.13	0.08
Esophageal appendix							
Length	0.70	0.65	0.52	0.47	0.43	0.50	0.44
Ratio to length of esophagus	1 : 7.4	1 : 7.5	1 : 7.6	1 : 8	1 : 8.3	1 : 5.7	1 : 6
Intestinal cecum							
Length	4.12	4.19	3.19	2.94	2.72	2.35	2.02
Ratio to length of esophagus	4 : 5	4 : 4.7	4 : 5	4 : 5	4 : 5.2	4 : 4.7	4 : 5.3
Tail							
Length	0.22	0.22	0.14	0.14	0.15	0.14	0.10
Nerve ring							
Distance from anterior end of esophagus	0.37	0.46	0.52	0.37	0.39	0.36	0.30
Vulva							
Distance from anterior extremity	11.71	12.65	....	....	....	....	....
Ratio to body length	1 : 3	1 : 2.8					
Spicules							
Length	....	....	1.9	1.8	1.9	1.54	0.78

Female: Maximum observed length about 35 mm. Vulva near point marking beginning of second third of body length. Tail short, acute, lacking terminal spike or other specialized cuticular or hypodermal processes (Fig. 4). Eggs in utero slightly oval, about 50 μ by 60 μ.

Male: Maximum observed length about 25 mm. Cuticle of ventral surface in caudal region with numerous longitudinal intrastrial ridges. Tail short, terminating in a rather pointed tip. Preanal papillae about 60 to 70 pairs; each subventral linear series arranged in a single row, except that occasionally a few pairs may form two rows immediately in front of the cloaca. Three or four pairs of adanal papillae present (Figs. 6–7). Postanal papillae usually 11 pairs, typically distributed as follows: A subterminal group of 2 subventral and 3 sublateral pairs; 6 subventral pairs in area between subterminal group and a transverse line through the posterior edge of the cloaca, the arrangement on each side being two papillae united to form a double papilla, one single papilla lateral to postero-lateral and three antero-lateral to double papilla (Fig. 6). The middle pair of the 3 subterminal sublateral pairs may be phasmids. Spicules approximately equal; about 1.7 to 1.9 mm long in apparently fully grown specimens, ranging down to about one-half this length in young specimens.

Hosts: Mycteria americana (=*Tantalus loculator*); *Anhinga anhinga; Ardea herodias.*

Location: Esophagus (?) and stomach.

Distribution: Brazil; United States (Arkansas, Florida, National Zoological Park, District of Columbia.).

Specimens: U. S. N. M. Helm. Coll. 30593; 30600; 31654.

Some of the specimens (U.S.N.M. No. 30593) upon which the above redescription is based were identified by Dr. E. B. Cram. None of the specimens are from the type host of von Drasche's species; however, in position and number the male postanal papillae correspond very closely with von Drasche's description and the lips and interlabia resemble those figured by him. It will be noted that in the females the vulva was in the anterior part of the body; in the specimens which Skrjabin regarded as identical with *C. multipapillatum* (von Drasche) the vulva was situated at the beginning of the posterior third of the body length.

So far as the writer has been able to determine, von Drasche's species is valid. It cannot be denied that no disposition has yet been made of some of the old specific names combined with *Ascaris,* but nearly all of the species which were recognizable from their descriptions now have been redescribed, allocated to proper generic positions, or relegated to synonomy. Thus far, it has not been suggested that *C. multipapillatum* is identical with any species named earlier.

The arrangement of the male postanal papillae in *C. multipapillatum* approaches that described for *C. granulosum* and *C. osculatum.* In one male examined by the writer, the pericloacal papillae formed two longitudinal series on each side of the cloaca much more definitely than is shown in Fig. 6; not only were the 4 single postanal papillae involved, but also the adanal papillae and the first 4 precloacal papillae. Thus, the similarity to the distribution of the pericloacal papillae in *C. osculatum,*

according to the figures of some authors, was striking. However, from a detailed comparison of the writer's specimens with available descriptions of *C. granulosum* and *C. osculatum* it appears that there are constant differences in the number and distribution of the postanal and preanal papillae in males of the three species and that there also are other differences of specific value.

According to Cram (1927) and Baylis and Daubney (1922), the male of *C. rosarium* (Connal, 1912) was described as having but three pairs of postanal papillae. Nevertheless, the latter authors identified some immature specimens from *Nyticorax griseus* as Connal's species, although they found 9 pairs of postanal papillae on the tail of an immature male. The arrangement of the papillae in the group just posterior to the cloaca of the male, as figured by Baylis and Daubney, is similar to that found in *C. multipapillatum* and it is quite possible that *C. rosarium* of Baylis and Daubney (1922) may be identical with *C. multipapillatum*.

Hsü (1932) commented on the variation in the number and arrangement of the male caudal papillae in specimens identified by him as *C. spiculigerum;* one of his illustrations (Pl. 1; Fig. 6) of the tail of a male specimen from a cormorant is very suggestive of *C. multipapillatum*. *C. andersoni* Vevers, 1923, also seems to resemble *C. multipapillatum*.

Contracaecum ainterlabium n. sp.

It is considered expedient at present, for reasons which cannot appropriately be explained here, to retain in the genus *Contracaecum* the species described by Skrjabin as *"Contracoecum multipapillosa,"* although it lacks interlabia and hence does not completely conform to the generic diagnosis, as was noted by Skrjabin. However, a new name must be proposed for the species as will be evident from the following discussion.

Skrjabin attributed the specific name *"multipapillosa"* to von Drasche in connection with the citation of a reference to the latter's paper and elsewhere he referred to *"Ascaris multipapillosa* Drasche 1882." Although subjectively a mere misspelling is involved, objectively Skrjabin applied a new name to von Drasche's species. The first name applied to a species is the valid name and *Ascaris multipapillosa* Skrjabin, 1916, is a synonym of *Ascaris multipapillata* von Drasche, 1882, as has been indicated elsewhere in this paper. The name *multipapillosa* hence is not available for Skrjabin's species, regardless of generic allocation, because its status is that of a rejected synonym (Internat. Rules Zool. Nomenclature, Art. 36). Skrjabin's species, if valid, is hence unnamed.

Therefore, since so far as can be determined, the species described by Skrjabin (1916) from *Ardea* sp. is not identical with any previously described, the designation *Contracaecum ainterlabium* n. sp. (syn. *Con-*

tracaecum multipapillosa Skrjabin, 1916 [= *Contracoecum multipapillosa* (Drasche 1882) of Skrjabin (1916)]; nec *Ascaris multipapillosa* Skrjabin, 1916 [= *Ascaris multipapillosa* Drasche 1882 of Skrjabin (1916)]; nec *Ascaris multipapillata* von Drasche, 1882) is proposed for it.

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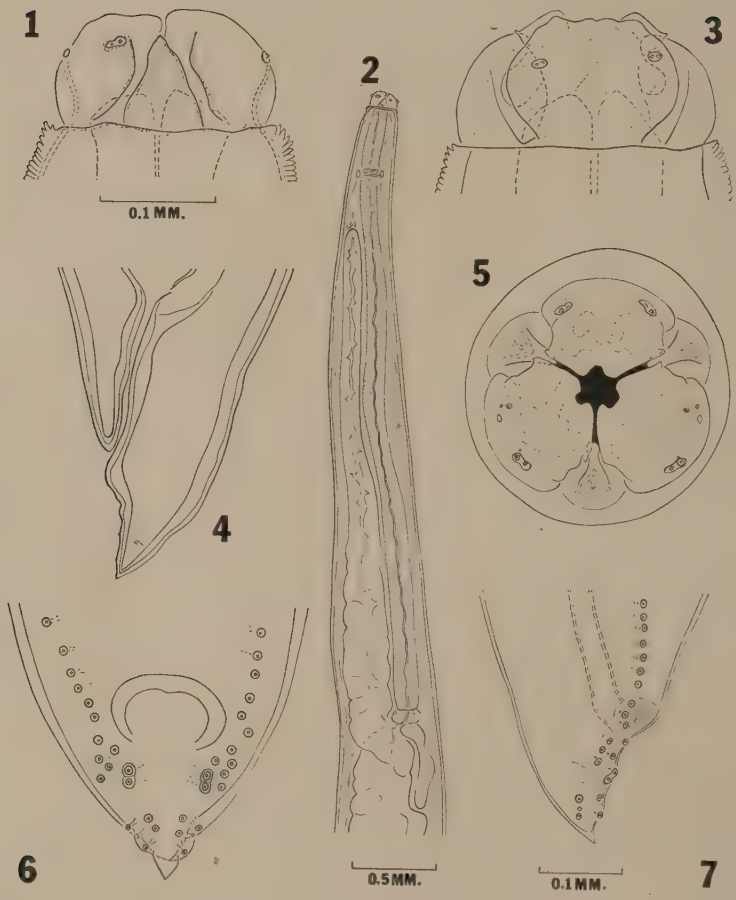

Contracaecum multipapillatum

FIG. 1. Latero-dorsal view of head of male specimen showing shape of interlabium.

FIG. 2. Lateral view of anterior region of male specimen showing muscular esophagus, esophageal ventriculus and appendix, and intestinal cecum.

FIG. 3. Dorsal view of head of female specimen showing shape of dorsal lip and of interlabia; to simplify the figure the outlines of the subventral lips are omitted. (Same scale as Fig. 1.)

FIG. 4. Lateral view of posterior extremity of female specimen. (Scale one-half that of Fig. 1.)

FIG. 5. *En face* view of head of male specimen. (Same scale as Fig. 1.)

FIG. 6. Ventral view of tail region of male specimen showing postanal, adanal, and a few preanal papillae. (Scale one-half that of Fig. 1.)

FIG. 7. Sublateral view of tail region of male specimen showing postanal, adanal, and a few preanal papillae.

THE ABSENCE OF OPALINIDS FROM THE ADULT GREEN FROG, *RANA CLAMITANS*

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Opalinas do not ordinarily occur in the adult green frog *Rana clamitans*. In examinations of over 200 green frogs I have not found them harboring infections of opalinids. This absence has been discussed by Metcalf (1923), Van Orden and Nelson (1926), and Hegner (1932). Metcalf (1923) states that possibly the opalinids are adapted only to the tadpole stage; that since this species of frog remains for two years in the tadpole stage, the cysts are passed from tadpole to tadpole. Van Orden and Nelson (1926) have suggested that opalinids have only recently entered *Rana clamitans* and are only in the process of adaptation to the adult stage of this frog. Hegner (1932) suggests that digestive secretions of *Rana clamitans* render the rectum of the adult frog unfavorable to opalinids.

In the present investigation, experiments were conducted to determine if opalinids would live when transferred to adult *Rana clamitans* by cloacal injection. Transfers were made in a solution of Pütter's fluid with powdered egg albumen by means of a small pipette. Injections were made into the recta of 20 frogs.

In no case were infections found later than 5 days after inoculation. In the majority of cases the opalinids disappeared 3 days after inoculation. These results agree with Hegner (1932) who, using similar methods, recovered a few opalinids from the rectum of 4 specimens of *Rana clamitans* 2 or 3 days after inoculation. On the contrary, Van Orden and Nelson (1926) found good infections of *Opalina* in two specimens of *Rana clamitans,* 162 and 174 days respectively after inoculation. It is interesting to note that these men treated the rectal contents with magnesium chloride before inoculation. Trichomonads and the fluke *Diplodiscus temperatus* which are often present in frogs would have been removed by this treatment as results in this laboratory show. These parasites were not mentioned by the above authors.

Trichomonas in relation to *Opalina*

In view of the results obtained by Van Orden and Nelson, studies were made of the incidence and number of *Trichomonas* in 19 species of amphibia. It was found that *Trichomonas* was a common inhabitant of the recta of amphibia in general, and that it was especially abundant in

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the green frog, *Rana clamitans,* as well as in various salamanders. Examination of over 100 green frogs, and 87 salamanders showed their recta to be swarming with infections of this flagellate. Also, frogs and toads harboring both *Opalina* and *Trichomonas* showed the number of these two parasites to be roughly in inverse proportions; those hosts harboring a heavy infection of *Opalina* showed a very light infection of *Trichomonas,* while hosts harboring light infections of *Opalina* carried heavy infections of *Trichomonas.* This numerical relationship was also observed in the case of rectal material from several specimens of *Hyla crucifer* and *Rana pipiens* tadpoles which were fed on a carbohydrate diet. Both species usually harbored a heavy infection of opalinids with few trichomonads; however, a carbohydrate diet usually promoted a heavy trichomonad infection in which case the opalinid infection disappeared. In individuals where the diet failed to produce heavy trichomonad infections the opalinid infection remained.

Diplodiscus temperatus IN RELATION TO *Opalina*

While studying the possible relationship of *Trichomonas* to opalinids in the green frog, it was observed that the trematode, *Diplodiscus temperatus,* was also usually present. After examination of many Ohio green frogs, several individuals of the same species were examined from Louisiana. In all of these frogs the fluke was found to be a common inhabitant. After continued observation of the green frog, and other amphibia as well, it was found that *Diplodiscus* and *Opalina* did not occur simultaneously in the same host. Furthermore, it was found that this fluke occurred in only a small percentage of green frog tadpoles, but that when present the opalinids were invariably absent. Experiments were therefore planned for a detailed study of the relations of these two parasites.

For these experiments tadpoles of the green frog were used. The tadpoles of this species are generally infected with opalinids; however, all the tadpoles from a certain small stream in Clinton County, Ohio, were found to be uniformly and entirely free from these ciliates. About 90 per cent of these tadpoles were infected with *Diplodiscus* with an average of about four flukes in each host. The smallest tadpoles, making up about 10 per cent of the collection, were free from flukes.

Approximately 50 tadpoles from this stream were fed cysts of *Opalina obtrigonoidea* Metcalf (1923), from the leopard frog, *Rana pipiens.* To infect these tadpoles, an entire rectum, containing active opalinids and cysts, was removed from an adult *R. pipiens* and placed in the vessel containing the experimental tadpoles, which fed freely upon this material. The adult opalinids if ingested died before reaching the rectum. Ingested cysts reached the rectum in about 5 hours where they were

observed either in the process of hatching or as excysted individuals measuring from 34 to 40 microns in length. Examination of flukes from these tadpoles showed their intestinal crura to be filled with these small opalinids (Fig. 1). When the flukes were placed in distilled water

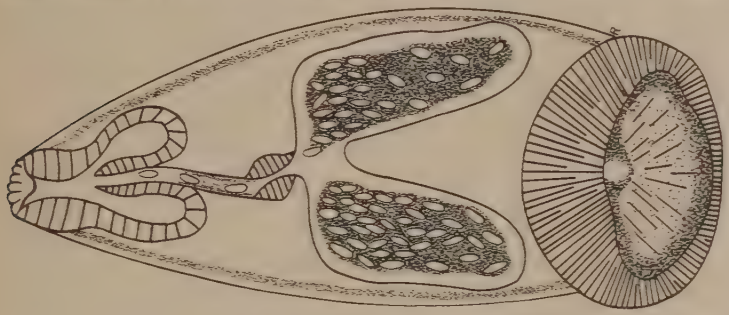

FIG. 1. Camera lucida drawing of *Diplodiscus temperatus*, details omitted. Opalinids, measuring 34 to 40 microns in length, are shown in the intestine having been ingested by the fluke soon after their excystment. Cilia are not shown.

their intestinal contents were regurgitated making possible a more accurate identification of these ciliates. Many of these protozoa in the lower part of the fluke's intestine were dead, other more recently ingested individuals near the esophagus were still moving about. In all cases the opalinids disappeared from the tadpoles in three days unless flukes were absent. As previously mentioned the smallest tadpoles did not harbor flukes and the opalinid infection of these was usually heavy and remained until they were killed and examined. In fact, the opalinids in these tadpoles grew to about 175 microns in length, dividing occasionally and forming cysts.

These experiments were repeated several times, and the observations on *Diplodiscus* confirmed on each occasion.

Experiments were next conducted to transfer flukes to the rectum of frogs harboring opalinid infections. Flukes were removed from both the adults and tadpoles of *Rana clamitans*, placed in Pütter's fluid and injected by means of a small pipette into the recta of a series of swamp cricket frogs, *Acris gryllus*, all of which contained opalinids. One fluke was transferred to each of 23 frogs which were opened 2 to 7 days after injection. In 10 specimens the fluke failed to establish itself and was not recovered, apparently having been carried out of the rectum with the fecal matter. Normal infections of opalinids remained in these 10 specimens. From 13 specimens the fluke was recovered and very few or no opalinids remained in the recta of these frogs. Four of the recovered flukes contained entire opalinids, and fragments of partly digested individuals.

Recently 8 tadpoles of *Rana clamitans* out of a series of 75 examined have offered additional evidence which confirms the observations on this relationship between the protozoa and the fluke. These 8 tadpoles showed simultaneous infections of flukes and opalinids. The opalinid infection in all cases was light while examination of the intestinal contents of the flukes showed the presence of opalinids in various stages of digestion. It is interpreted that these tadpoles had just recently become infected with the fluke and if the examinations had been made at a later period no opalinids would have been found. Incidentally, three specimens of *Nyctotherus cordiformis* were also present in one fluke and these still exhibited locomotion.

SUMMARY

On the basis of this study it is evident that *Diplodiscus* is partly responsible for the absence of opalinids from the adult green frog, *Rana clamitans*. Observations supporting this statement are as follows: (1) *Diplodiscus* ingests opalinids when they are present; (2) in localities studied by me the incidence of opalinid infection is very high in the green frog tadpoles, whereas the incidence of fluke infection is low; (3) conversely, the incidence of opalinid infection is practically nil in the adult green frogs, whereas the incidence of fluke infection is very high; (4) when flukes are transferred to the rectum of opalinid infected *Acris gryllus* by cloacal injection, the opalinids are reduced in number or completely disappear; (5) *Trichomonas* and *Opalina* in frogs and toads occur in roughly inverse proportions. A carbohydrate diet increases the number of trichomonads and decreases the number of opalinids.

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ACOLPENTERON URETEROECETES FISCHTHAL AND ALLISON, 1940, A MONOGENETIC TREMATODE FROM THE URETERS OF THE BLACK BASSES, WITH A REVISION OF THE FAMILY CALCEOSTOMATIDAE (GYRODACTYLOIDEA)*

JACOB H. FISCHTHAL AND LEONARD N. ALLISON

Acolpenteron ureteroecetes, a monogenetic trematode belonging to the superfamily GYRODACTYLOIDEA, was first discovered by one of us (Fischthal) in the fall of 1939 in the ureters and urinary bladder of the large-mouthed bass, *Huro salmoides* (Lacépède). Since many parasites are common to both this species and the northern small-mouthed bass, *Micropterus dolomieu dolomieu* Lacépède, the latter were examined for this trematode and some were found to be infected.

This is the first record of a monogenetic trematode from the ureters or urinary bladder of fishes. Previously, such trematodes from the urinary bladders have been from frogs and turtles.

A preliminary description of this new genus and species has appeared in an abstract by Fischthal and Allison (1940).

Genus *Acolpenteron* Fischthal and Allison, 1940

Generic diagnosis: Monopisthocotylea. Head lappets, eyes and anchors absent. Haptor cup-like, possessing 14 marginal hooklets. Sensory hairs present, arising from papillae. Testis single, elongated. Ovary elliptical, median. Vagina ventral, near right margin of body. Intestinal crura joined posteriorly, without diverticula.

Type species: Acolpenteron ureteroecetes Fischthal and Allison, 1940.

Acolpenteron ureteroecetes Fischthal and Allison, 1940
(Figs. 1–5)

Specific diagnosis: Acolpenteron. Adults, 0.931 × 0.105 mm. Haptor, 0.057 × 0.096 mm. Hooklets, 0.023 mm long. Testis elongated, 0.053 × 0.016 mm. Seminal vesicle and coarse and hyaline prostates at left of, and opening into cirrus. Vas deferens sinistral, looping over prostates. Cirrus (0.045 mm long) with forked accessory piece; male opening mid-ventral. Ovary (0.062 × 0.038 mm) thick posteriorly, thin anteriorly. Oviduct, yolk ducts and seminal receptacle uniting anterior to ovary. Mehlis' gland large, extending from oötype to anterior third of testis. Uterus opening near cirrus. Vagina bent, opening ventral, near right margin posterior to cirrus. Seminal receptacle present. Vitellaria voluminous, extending from pharynx nearly to haptor. Pharynx muscular, 0.047 mm in diameter. Esophagus short. Intestinal crura without diverticula, confluent posteriorly.

Eggs (0.075 × 0.056 mm) operculate, anopercular process short, sharply bent and knobbed; 1 egg in uterus at a time; found free in ureters and urinary bladder of hosts; passed with urine in single-celled stage; hatching in water after 6–9 days. Larva (0.143 × 0.020 mm) ciliated, the cilia arising from 4 groups of cells at ends

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* Contribution from the Department of Zoology, University of Michigan.

and middle of sides of body; 4 eyes present, their lenses facing laterally; anterior pair of eyes 0.006 mm in diameter, posterior pair 0.008×0.010 mm; 14 hooklets (0.013 mm long) on cup-like haptor (0.042×0.050 mm); pharynx muscular, 0.015 mm in diameter; head lappets and anchors absent; swimming path a long spiral, rotating to the right.

Hosts: Huro salmoides (Lacépède) and *Micropterus d. dolomieu* Lacépède.

Locations: Ureters and urinary bladder.

Localities: Huron River, Honey Creek, Whitmore Lake and West Lake in Washtenaw County, Michigan.

Type and Paratypes: U. S. Nat. Mus. Helm. Coll. No. 42096 and No. 44301.

Examination of 175 large- and small-mouthed basses varying in size from two inch fingerlings to 14 inch adults showed that approximately 36 per cent of these fish are infected with *A. ureteroecetes* (Table 1).

TABLE 1.—*Incidence of infection and habitat preference of* Acolpenteron ureteroecetes

Locality	No. examined	No. inf.	% inf.	No. with worms in ureters only	No. with worms in bladder only	No. with worms in both places
Huro salmoides (Lacépède)—large-mouthed bass						
Huron River ...	52	30	58	21	6	3
Saline River ...	5	0	0	0	0	0
Honey Creek ...	20	2	10	2	0	0
Whitmore Lake .	35	8	23	7	1	0
West Lake	3	3	100	3	0	0
Winan's Lake ..	3	0	0	0	0	0
Totals	118	43	36	33	7	3
				(77% of the 43 infected)	(16% of the 43 infected)	(7% of the 43 infected)
Micropterus d. dolomieu Lacépède—northern small-mouthed bass						
Huron River ...	42	15	36	11	2	2
Saline River ...	7	0	0	0	0	0
Whitmore Lake .	8	5	63	4	0	1
Totals	57	20	35	15	2	3
				(75% of the 20 infected)	(10% of the 20 infected)	(15% of the 20 infected)

The data also indicate that approximately 76 per cent of the infected black basses harbor worms only in the ureters, thus demonstrating a much greater predilection for the ureters as a habitat.

The black basses are usually infected with one to five worms. However, occasional heavy infections of 22, 39, and 52 adults, respectively, were found. In the latter case the worms were considerably crowded and several were found in the uriniferous tubules which empty directly into the ureters. No pathological conditions were observed.

The ureters and urinary bladders of fishes probably are more common habitats for monogenetic trematodes than is supposed by investigators in this field. We base this on the finding of *A. ureteroecetes* in these habitats in the black basses, and also on the more recent finding of another new species in the ureters of another species of fish.

Family Calceostomatidae (Parona and Perugia, 1890)

Price (1937) emended the family characters of the Calceostomatidae (Parona and Perugia, 1890) as follows: "Cephalic gland ducts not concentrated into head organs but remaining scattered over a considerable area on either side of anterior end of body, the anterior end being expanded and forming head lappets. Haptor sucker-like but not strongly muscular, with or without large hooks, with or (?) without marginal hooklets. Intestine with short diverticula. Eyes present or (?) absent. Testis single. Cirrus simple, cuticularized. Vagina present or absent."

Genera recognized as belonging to this family are *Calceostoma* Beneden, 1852 and *Fridericianella* Brandes, 1894. It is the opinion of Dr. E. W. Price of the Bureau of Animal Industry and of ourselves that the genera *Acolpenteron, Anonchohaptor* Mueller, 1938 and *Anoplodiscus* Sonsino, 1890 should also be placed in this family (see discussion below). In order to accommodate these three genera, the family diagnosis must be further emended as follows:

Family Calceostomatidae (Parona and Perugia, 1890)
Char. emend.

Synonym: Calceostomidae Parona and Perugia, 1890.

Diagnosis: Ducts of cephalic glands not concentrated into head organs but remaining scattered over a considerable area on either side of anterior end. Anterior end expanded and forming head lappets, or not expanded and head lappets absent. Haptor sucker-like but not strongly muscular, with or without large hooks, with or without marginal hooklets. Intestine with or without short diverticula. Eyes present or absent. Testis single. Cirrus simple, cuticularized. Vagina present or absent.

Type genus: Calceostoma Beneden, 1852.

Key to Genera of Calceostomatidae

1. Pair of pseudosuckers present at anterior end of body. *Anoplodiscus* Sonsino
   Pseudosuckers absent at anterior end of body ..... 2.
2. Vagina absent ..... *Calceostoma* Beneden
   Vagina present ..... 3.
3. Head lappets absent ..... *Acolpenteron* Fischthal and Allison
   Head lappets present ..... 4.
4. Eyes absent; ovary tubular, median ..... *Fridericianella* Brandes
   Eyes present; ovary loops around right limb of intestine. *Anonchohaptor* Mueller

Genus *Calceostoma* Beneden, 1852

Diagnosis: Anterior end of body expanded and forming large curled head lappets. Haptor cup-shaped, armed or (?) unarmed. Intestinal limbs with numerous short diverticula. Eyes present. Testis elongated. Ovary branched. Vagina absent.

Type species: Calceostoma calceostoma (Wagener, 1857) Johnston and Tiegs, 1922.

In this genus Price (1937) included three species, *C. calceostoma* (Wagener, 1857) (syn., *C. elegans* Beneden, 1858), *C. inerme* Parona and Perugia, 1889, and *C. glandulosum* Johnston and Tiegs, 1922, and stated that no representative of the genus has been reported from North America.

Genus *Fridericianella* Brandes, 1894

Diagnosis: Head lappets not as prominent as in *Calceostoma*. Haptor cup-like, with one pair of small centrally placed hooks; marginal hooklets (?) absent. Eyes absent. Intestinal branches with lateral diverticula, united by commissure posterior to testis. Testis single, rounded. Ovary tubular, median. Vagina present, opening laterally near equator of body.

Type species: Fridericianella ovicola Brandes, 1894.

Brandes (1894) described the type and only species from specimens collected from the eggs of *Arius commersonii* Lac., a fresh- and brackish-water fish from South Brazil.

Genus *Anoplodiscus* Sonsino, 1890

Diagnosis: Anterior haptors in form of a pair of pseudosuckers situated at anterior end of body. Posterior haptor cup-like, unarmed. Eyes present. Intestine without diverticula, united by a commissure posterior to testis. Testis single, preequatorial. Ovary round, pretesticular. Vagina ventral, near right margin.

Type species: Anoplodiscus richiardii Sonsino, 1890.

Sonsino (1890) described the type species, *A. richiardii* from the gills of *Pagrus orphus* from the Mediterranean. Monticelli (1905) subsequently redescribed this species. The only other species so far included in this genus was described by Johnston (1930) as *A. australis* from the fins of *Sparus australis*, at Sydney Harbor, Australia.

Monticelli placed the genus *Anoplodiscus* in the Anisocotylinae Monticelli, 1903—a subfamily without a corresponding genus and consequently invalid—and later Tagliani (1912) erected for it the subfamily Anoplodiscinae, elevating Monticelli's invalid Anisocotylinae to the status of an invalid family Anisocotylidae. Johnston and Tiegs (1922) considered *Anoplodiscus* as possibly belonging to the Calceostomatidae, subfamily Dionchinae, while Fuhrmann (1928) and Gallien (1937) placed it in the Monocotylidae, subfamily Pseudocotylinae. Price (1938) included ". . . *Anoplodiscus* in the Microbothriinae (family Microbothriidae, superfamily Capsaloidea), mainly because the general organization and the lack of haptoral hooks suggest relationship with such genera as *Microbothrium, Leptocotyle* and *Leptobothrium*. On the other hand, the presence in *Anoplodiscus* of eyes and a cirrus with accessory piece suggests affinities with genera of the Gyrodactyloidea. It is possible that a restudy of the species of *Anoplodiscus* may show the haptor to be armed with minute hooks in which case it should be transferred to the family Calceostomatidae (Gyrodactyloidea)."

In a personal letter, Dr. E. W. Price makes the following comments:

"I have examined the specimens of the monogenetic fluke (*Acolpenteron ureteroecetes*) . . . and am of the opinion that they represent a new genus perhaps closely related to *Anoplodiscus*. In my paper (1938, J. Wash. Acad. Sc. **28**: 187–188) I have discussed the systematic position of the genus *Anoplodiscus*. This genus was placed by me in the family Microbothriidae, subfamily Microbothriinae. . . . My present opinion is that *Anoplodiscus* and your new form (*Acolpenteron*) should be placed in the Calceostomatidae (Gyrodactyloidea)."

Genus *Anonchohaptor* Mueller, 1938

Diagnosis: Prominent head lappets present. Haptor disc-like without large hooks, but possessing 14 hooklets, 12 marginal and 2 central. Four eyes present. Intestine without diverticula, united by commissure posterior to testis. Testis single, small. Ovary looping around right limb of intestine. Vagina ventral, on right margin.

Type species: Anonchohaptor anomalum Mueller, 1938.

This genus contains only the type species which was described by Mueller (1938) from the gills of suckers from Chautauqua Lake, N. Y. Mueller (1938) records the following comments contained in a personal letter from Dr. E. W. Price: "This worm (appears to have) characters of both the superfamilies Gyrodactyloidea and Capsaloidea. In some respects it is quite like *Fridericianella,* if allowance be made for possible errors of observation by Brandes. The looping of the ovary around one of the intestinal limbs is more or less constant character of the Monocotylidae (Capsaloidea). The absence of large hooks (anchors) and bars is characteristic of *Fridericianella,* although eyes are supposed to be missing in the latter genus. The H-like formation of the gut is like both *Fridericianella* and *Anoplodiscus*. The nature of the copulatory organ is definitely of the type occurring in the Gyrodactyloidea (Dactylogyridae and Calceostomatidae) and not that of Capsaloidea. The anterior end of this form seems more capsaloid than gyrodactyloid. Personally, I am rather of the opinion that the form should be referred to the Calceostomatidae (Gyrodactyloidea)."

SUMMARY

1. *Acolpenteron ureteroecetes* originally described by Fischthal and Allison (1940) is described in further detail.

2. This is the first monogenetic trematode to be recorded from the ureters or urinary bladders of fishes.

3. Approximately 36 per cent of the large- and small-mouthed basses examined from Washtenaw Co., Michigan, were infected with this species; approximately 76 per cent of the infected fishes harbored this trematode in the ureters only.

4. It is our belief that the ureters and urinary bladders of fishes are more common habitats for monogenetic trematodes than is supposed by

investigators in this field. This is based not only on the finding of *A. ureteroecetes* in these habitats in the black basses but on the more recent finding of an additional new species in the ureters of another species of fish.

5. The family CALCEOSTOMATIDAE (Parona and Perugia, 1890) has been emended, and to it are now ascribed the genera *Acolpenteron* Fischthal and Allison, 1940, *Anonchohaptor* Mueller, 1938, and *Anoplodiscus* Sonsino, 1890, in addition to the previously included genera *Calceostoma* Beneden, 1852, and *Fridericianella* Brandes, 1894.

6. A key to the genera of the family CALCEOSTOMATIDAE is presented.

7. The diagnosis of each genus is followed by a list of species and a brief discussion.

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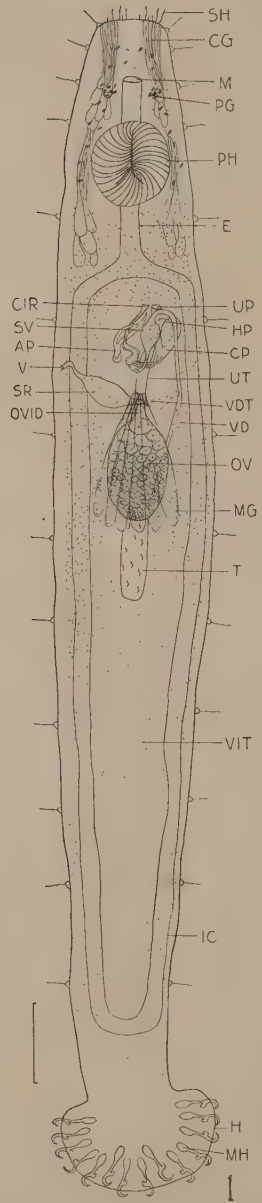
EXPLANATION OF PLATE, p. 524

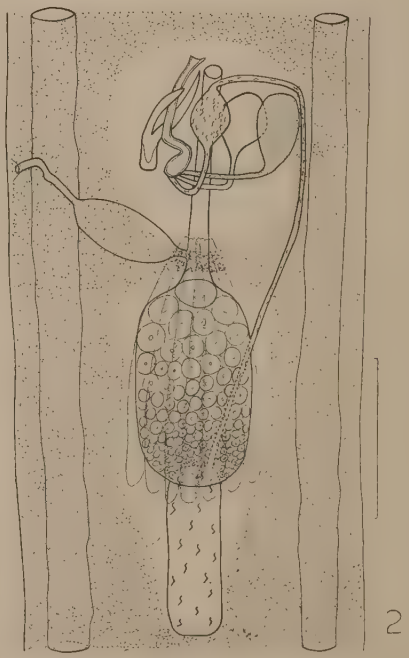
All figures refer to *Acolpenteron ureteroecetes*. The value of the scale is 0.05 mm for Figs. 1, 2 and 5, and 0.02 mm for Fig. 3.

ABBREVIATIONS

AP	accessory piece	PG	pigment granules of disintegrated eyes
CG	cephalic glands	PH	pharynx
CIR	cirrus	SH	sensory hair
CP	coarse prostate	SR	seminal receptacle
E	esophagus	SV	seminal vesicle
H	haptor	T	testis
HP	hyaline prostate	UP	uterine pore
IC	intestinal ceca	UT	uterus
M	mouth	V	vagina
MG	Mehlis' gland	VD	vas deferens
MH	marginal hooklet	VDT	vitelline duct
OV	ovary	VIT	vitellaria
OVID	oviduct		

FIG. 1. Adult worm, ventral view.
FIG. 2. Reproductive complex, enlarged, ventral view.
FIG. 3. Cirrus and accessory piece.
FIG. 4. Marginal hooklets.
FIG. 5. Hatched egg showing operculum and posterior process.





Acolpenteron ureteroecetes

STUDIES ON THE MORPHOLOGY AND BIOLOGY OF A PSILOSTOME FLUKE*

SEYMOUR I. FELDMAN

During the late fall of 1939, approximately one hundred *Stagnicola reflexae* were brought into the laboratory supposedly infected with an echinostome cercaria. Careful study, however, showed that they were infected with a psilostome cercaria, closely related to the echinostome group, but lacking the collar of spines.

In checking the literature for the described species of closely related cercariae, the writer came upon one described by Cort (1914) as *Cercaria reflexae,* from *Lymnea reflexae* (= *Stagnicola reflexae*) from the vicinity of Chicago, Illinois. This cercaria resembled the one found at Edina, Minnesota, to a remarkable degree. However, since flame cell patterns were unknown at the time of this description (Cort, 1914), it was impossible to compare the two forms in this respect. Nevertheless, the writer is firmly convinced that they are identical.

Sewell (1922) placed *Cercaria reflexae* together with the cercaria of *Himasthla militaris* in the "Reflexae" group. The latter species is an echinostome which shows no spines in the cercarial stage, but has a very distinct collar of spines in the adult. Although Sewell recognized the close relationship between these two cercariae, in view of our present knowledge, he was incorrect in asserting that *Cercaria reflexae* was probably a larval stage of a species of the genus *Himasthla.*

MATERIAL AND METHODS

The cercariae and rediae were best studied in the living condition. For the detailed morphology of the excretory system, cercariae were stained vitally with neutral red and Nile blue sulphate, and studied under a vaseline-ringed coverslip. Measurements of the cercariae were all taken from specimens fixed in the following manner: cercariae were set in a refrigerator (38° F) for 3 to 4 hours, after which time they were fixed in hot Gilson's fluid. This method was found to be very satisfactory for fixing cercariae in the extended condition. Fixed specimens were then stained with Mayer's paracarmine, dehydrated, cleared in methyl salicylate and mounted in clarite. Rediae were fixed in alcohol-acetic-formalin (A.F.A.), stained and mounted as described above.

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The adult trematodes secured in the course of the experimental work were studied in the living and fixed condition. They were fixed in A.F.A. and in hot Gilson's fluid, and stained with Semichon's acetic carmine, Ehrlich's acid haematoxylin and Mayer's paracarmine. The worms were then dehydrated through the alcohols, cleared in methyl salicylate and mounted in clarite. The adults were also fixed in Bouin's fluid, sectioned and stained with Ehrlich's haematoxylin-eosin or Delafield's haematoxylin-eosin.

EXPERIMENTAL RESULTS

All cercariae used in the experiments were obtained from naturally infected *Stagnicola reflexae*. The metacercariae of *Psilostomum reflexae* (the adult stage of *Cercaria reflexae*) were found naturally in *Stagnicola reflexae* and *Physa gyrina*. These two snails and *Heliosoma* sp. were experimentally infected with the cercariae in the laboratory. Many attempts were made to infect laboratory-reared tadpoles, but all were unsuccessful. Laboratory-reared snails of the species mentioned above were all infected in the following manner: two snails were placed in an isolation bottle with an infected *Stagnicola reflexae* producing large numbers of cercariae for 48 hours, after which time they were removed to another container. In each case the cercariae penetrated the snail and encysted in the mantle cavity; the metacercariae were readily seen macroscopically as white spheres against the black pigmented mantle cavity. They were infective five to seven days after encystment.

After feeding infective metacercariae to young chicks, mature worms were found in the small intestine, two to three inches in front of the caecum, five days after infection. One chick was autopsied eleven hours after infection and four young worms showing well-developed testes and the beginning of the development of the ovary and cirrus pouch were recovered.

Several species of birds and mammals were used in infection experiments with positive results only in chicks. Forty-seven chicks of several breeds were used in this series of infection experiments. The majority were infected soon after hatching and before being fed. Of the forty-seven chicks fed metacercariae, 18 or 38.3% were found parasitized at autopsy. From these 18 infected chicks, 59 worms or 3.2 worms per infected chick were obtained, although an average of 150 metacercariae were fed each chick. From these experiments, it became apparent that the chick was not a very satisfactory host for this trematode, since only 2% of the metacercariae fed developed.

Larson et al (1939), showed that the body temperature of mice could be raised from 100.6° F to 104.1° F if they were kept in a chamber at 98° F for three days. Reasoning along these lines, the writer attempted to approach avian temperatures in mice by this procedure, in order to de-

termine if a bird trematode might be made to mature in a mammal whose body temperature closely approximated that of a bird. Three mice were used in this experiment. Their body temperatures were raised by the procedure described above and they were then fed the metacercariae and maintained at 98° F. Three days later they were autopsied, and all mice were negative.

Psilostomum reflexae

The Cercaria

(Figs. 3, 4, 5)

Description: Relaxed, the body of the cercaria is elongate, sides more or less parallel with a slight tapering at the anterior end. Oral sucker powerful, terminal and slightly oval in outline 0.039–0.054 mm (mean 0.046 mm) long by 0.043–0.050 mm (mean 0.046 mm) wide. Acetabulum protrusible, considerably larger than oral sucker, 0.066–0.074 mm (mean 0.071 mm) in diameter, located just posterior to the mid body. Pharynx broadly oval, about one-half the diameter of the oral sucker; esophagus extends just anterior to the acetabulum where it bifurcates into the two intestinal caecae; the latter extend to the posterior end of the body. Ten to twelve cephalic duct openings present just anterior to the oral sucker.

Excretory bladder with one chamber; entire excretory system echinostome-like. Two large excretory siphons arise mesally with a common stem from the anterior end of the excretory bladder; siphons proceed laterally for a short distance and then anteriorly and dorsally in four loops to the posterior level of the acetabulum and continue again ventrally and anteriorly to the level of the pharynx in three or four short loops. The anterior part of each siphon contains many highly refractive granules. At the level of the pharynx the siphons make a wide loop and proceed posteriorly as the main excretory tubules to the posterior margin of the excretory bladder where they make another wide loop. The tubules proceed anteriorly to a short distance behind the acetabulum where they are no longer visible. The main collecting tubules are approximately one-half the diameter of the siphons. Twenty-eight flame-cell-like tufts or cilia were observed in the main collecting tubules. It was impossible to elucidate any flame cell pattern by any technique known to the writer because of the extensive distribution of the cystogenous glands. Forty-two pairs of flame cells and a median unpaired flame cell ventral to the posterior margin of the bladder were observed. Of these, nine pairs were found anterior to the fore margin of the acetabulum; thirty-three pairs were found scattered throughout the region posterior to the acetabulum. Tail 0.487–0.574 mm (mean 0.524 mm) by 0.052–0.070 (mean 0.061 mm) tapering posteriorly to a point; tail highly muscular. A narrow duct leads from the middle of the posterior margin of the excretory bladder into the tail region for a short distance where it bifurcates into a right and left fork at about one-third the tail length; no flame cells were observed in the tail. Tail provided with a dorsal and ventral fin fold which extends from the tip to the level of the excretory bifurcation.

The cercariae of *P. reflexae* were active swimmers, and under laboratory conditions remained motile for approximately twelve hours. Soon after, they settled to the bottom and crept along the surface of the isolation bottle in measuring-worm fashion with the aid of their powerful suckers for a short time. After fifteen hours most of the cercariae were dead. The cercariae emerged every morning between 6 and 10 AM, although in several instances they did not emerge until mid-afternoon. At these times it was observed that the intensity of light in the laboratory

was greatly reduced. Several experiments were attempted in order to determine if intensity of light had any significant effect on the time of emergence of the cercariae. In order to test this, one half of the infected snails were placed in a dark box and one half in front of a window. The snails left in the open were examined the following mornings and in all cases the cercariae had already emerged. The snails kept in the dark showed no swimming cercariae at the same time. Although this condition was observed on numerous occasions, available data do not justify a final conclusion regarding the effect of light intensity on the time of cercarial emergence.

The Redia

(Fig. 2)

Description: Body sacculate. Distinct collar with four lobes present in the anterior part of the body; birth pore located slightly posterior to one of the dorsal lobes. A pair of posterior locomotor appendages of variable size and activity are located at the posterior third of the body. Oral sucker poorly developed; large muscular pharynx situated just posterior to the oral sucker and terminal in position. Gut ventral, extending from the pharynx to the level of the locomotor appendages; filled with dark brown or orange brown granules. Germ balls and developing cercariae fill the entire body space of the rediae. Excretory system completely obscured by the developing cercariae.

The rediae of *P. reflexae* were studied from naturally infected *Stagnicola reflexae*. No mother rediae or sporocysts were observed. This was probably due to the fact that all the infected snails had infections of long duration. Daughter rediae were found in the liver, gonad, and kidney of the infected snail host in prodigious numbers, frequently destroying most of the tissue of these organs. When removed from the tissues, the rediae were of variable size; the older and larger were orange to brown in color, the younger and smaller forms colorless.

The Metacercaria

The metacercaria of *P. reflexae* differs from that of the closely related *P. ondatrae* Price, 1931 in the type of intermediate host utilized and in the thickness of the cyst wall. The former encysts in snails and has a three-layered cyst wall 0.039–0.042 mm wide, while the latter is characterized by a very thin cyst wall and is found in the lateral line canal and under the scales of several species of fish. The cysts of *P. reflexae* are spherical with a mean diameter of 0.259 mm while those of *P. ondatrae* are elongate and measure 0.32 mm by 0.21 mm. All attempts to excyst the metacercariae by rupturing the cyst wall or by means of artificial digestion methods were futile.

The Adult

(Fig. 1)

Description: Psilostomum: Body linguiform, bluntly rounded at either end. Length 1.46–1.83 mm (mean 1.47 mm); width remarkably uniform along most of

the body length, 0.42–0.62 mm (mean 0.46 mm). Entire surface beset with small triangular spines arranged in close alternate rows; spines become less numerous in the hind body. Two rows of cuticular spines in the region of the oral sucker distinctly separated from the rest of the body spines by a width of 0.02 mm; first of these two rows contains ten spines, second row twelve to fourteen. This latter condition is highly suggestive of the collar of spines found in the echinostomes. Oral sucker subterminal, 0.06–0.09 mm (mean 0.07 mm) in diameter. Acetabulum in anterior third of body, larger than oral sucker, 0.11–0.16 mm (mean 0.13 mm) in diameter. Prepharynx very short; pharynx oval, well developed, 0.05–0.07 mm (mean 0.06 mm) by 0.05–0.06 mm (mean 0.055 mm). Esophagus long, 0.20–0.23 mm (mean 0.22 mm), dividing to form the intestinal caecae just anterior to the acetabulum. Caecae increase in width as they extend toward the posterior part of the body. Excretory pore subterminal and ventral; bladder truncate; main tubules readily observable in the forebody of the living specimens as highly branched structures reaching the level of the pharynx.

Testes tandem, spherical or slightly oval, located in the middle of the hind body. Anterior testis 0.12–0.17 mm (mean 0.13 mm) by 0.11–0.20 mm (mean 0.18 mm); posterior testis 0.12–0.17 mm (mean 0.13 mm) by 0.14–0.21 mm (mean 0.19 mm). Cirrus pouch oval, slightly dorsal, either to the left or right of the acetabulum and never extending beyond its posterior margin. Seminal vesicle large, 0.13 mm in length, in some cases occupying most of the cirrus pouch; cirrus simple, slender and short. Prostate gland well developed. Genital pore situated between the acetabulum and the bifurcation of the intestine.

Ovary anterior to the testes, round or oval, slightly to the left of the median line of the body; diameter 0.09–0.11 mm (mean 0.10 mm). Shell gland present, well developed; yolk ducts pass to a voluminous yolk reservoir situated anterior to the anterior testis. Seminal receptacle and Laurer's canal not visible. Uterus short with few convolutions, containing six to eight eggs. Vitelline follicles large and closely distributed, extending to the level of the acetabulum on either side and converging posteriorly behind the hind testis to form a single compact mass filling most of the post-testicular region of the body. Eggs yellow-brown in color, 0.07–0.09 mm (mean 0.08 mm) by 0.05–0.06 mm (mean 0.056 mm).

Habitat: Small intestine.

Host: Domestic chicken (experimental).

Collateral types: U.S.N.M. No. 36762.

The above description of *P. reflexae* is based on a study of ten collateral types taken from the experimental chick host.

TAXONOMIC RELATIONSHIPS

The family PSILOSTOMIDAE was erected by Odhner in 1913 to include five genera of worms, all echinostome-like in their morphology and all parasites of birds. It was divided into two subfamilies, PSILOSTOMINAE Lühe, 1909 and ORCHIPEDINAE Skrjabin, 1913. The former subfamily, which includes the genera *Psilostomum* and *Psilochasmus,* is of chief interest here. The genus *Psilostomum* was erected by Looss in 1898 to include three species of worms. Of the original three, only the type species, *P. brevicolle* (= *platyurum* Mühling) still stands as valid.

Looss in his generic diagnosis, described the esophagus of *Psilostomum* as "fehlend oder sehr kurz." It was indeed unfortunate that he chose to describe this structure with so broad a term as "sehr kurz." In the eight known species of *Psilostomum,* the esophagus ranges from "no

esophagus" to one 0.324 mm in length (*P. arvicolae* Schulz and Dobrowa, 1933). *P. reflexae* falls somewhat between these two extremes, since its esophagus has a mean length of 0.22 mm. The problem of erecting a new genus for *P. arvicolae* and *P. reflexae* presented itself. After a careful study of the other morphological features, and after comparing these with similar characters in the recognized species of *Psilostomum,* it was not believed that there was any justification for erecting a new genus for this variation in morphology. Since the writer was unable to study any of the described species of *Psilostomum* with the exception of *P. ondatrae* Price, he has little choice but to accept them all as valid.

P. reflexae differs from *P. redactum* Nicoll, 1906, *P. varium* Linton, 1928 and *P. brevicolle* Creplin, 1829 by the presence of an esophagus. In the latter three species the esophagus is completely lacking. It also differs from *P. ondatrae* Price, *P. cygnei* Southwell and Kirschner, 1937 and *P. progeneticum* Wisniewski, 1932 by possessing an esophagus longer than 0.1 mm. *P. reflexae* differs from *P. arvicolae* Schulz and Dobrowa in that the latter lacks an oral sucker and has an acetabulum approximately 0.4 mm in diameter.

DISCUSSION

The life cycle herein described is the fourth known cycle of the PSILOSTOMIDAE. *P. reflexae* agrees morphologically and biologically with other psilostomes and echinostomes in their salient features. There are several specific differences in morphology mentioned in the text. *P. reflexae* is more host specific than any of its close relatives. *P. ondatrae* has been reported naturally from the muskrat, *Ondatra zibethica* and the California gull, *Larus californicus* by Price (1931) and from young chickens by Newsom and Stout (1933). It has also been reported from an osprey, *Pandion haliaetus carolinensis* and from Cooper's hawk, *Accipiter cooperi* by Beaver (1939) who also experimentally infected pigeons, chickens, ducks, and canaries. *Sphaeridiotrema globulus* has been found in a variety of ducks by Szidat (1937) and *Psilotrema spiculigerum* has been found in ducks, turtle doves, hens, quails, and mice by Mathias (1925).

The writer attempted to infect ducks, sparrows, pigeons, rats, guinea pigs, mice, rabbits, cats, and chicks. Only in the last mentioned hosts were the adults of *P. reflexae* recovered.

The echinostomes in general, are the least host specific of the trematodes known to the writer. This lack of host specificity is attested by the world wide distribution of these forms. From the small amount of work done with the psilostomes, it appears that they are more host specific than are the closely related echinostomes. As our knowledge of the trematode fauna of the world increases, we will be able to solve more of

the problems related to host specificity. At present, the nature of host specificity in the TREMATODA is to a very large extent a matter of conjecture.

SUMMARY

1. *Cercaria reflexae* Cort, 1914 was found in *Stagnicola reflexae* in the vicinity of Edina, Minnesota.

2. Rediae were found naturally in the same snail host. None of the larval stages in the primary snail host were produced experimentally.

3. Metacercariae were found naturally in the mantle cavity of *Physa gyrina* and *Stagnicola reflexae*. These two snails and *Heliosoma* sp. have been experimentally infected.

4. Metacercariae were found in the same snail which produced the cercariae. The former are infective five to seven days after encystment.

5. *Psilostomum reflexae* (Cort, 1914) was found in the small intestine of the chick after feeding the metacercariae. The adults mature in five days. No pathological anatomy was observed.

6. The natural host of this trematode is probably another snail eating bird, but as yet no natural infections have been found.

7. Eggs pass out with the feces in an early segmentation stage. Development occurs on the outside. Miracidia are not known.

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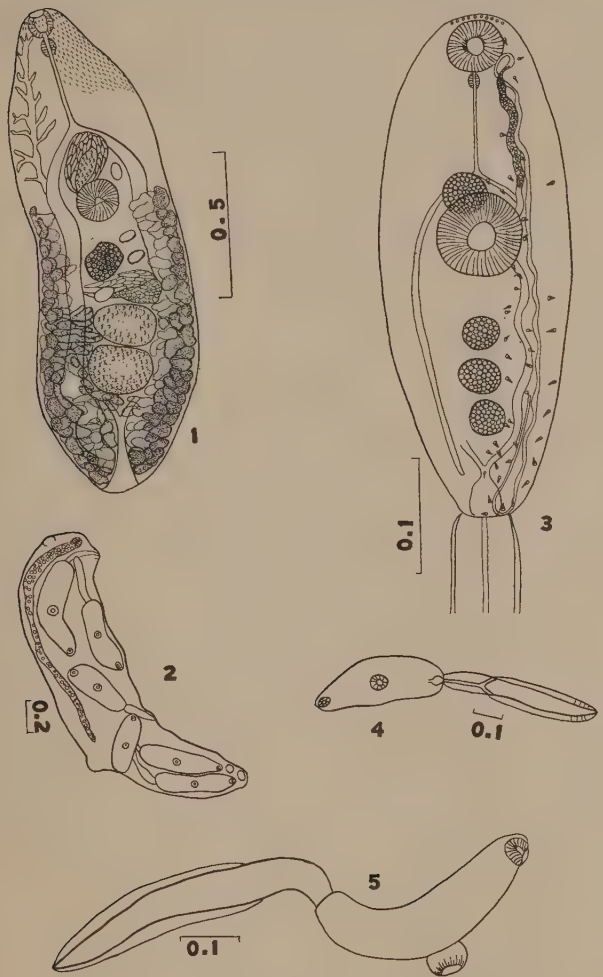

Fig. 1. Adult *Psilostomum reflexae* showing general morphology.
Fig. 2. Redia of *P. reflexae*.
Fig. 3. Cercaria of *P. reflexae* showing details of the excretory system.
Fig. 4. Cercaria showing excretory system of the tail region and the caudal fin folds.
Fig. 5. Cercaria showing protrusible acetabulum.

All scales in millimeters

THE "GOPHER," *CITELLUS RICHARDSONII* (SABINE), AS AN EXPERIMENTAL HOST FOR *TRICHINELLA SPIRALIS*

EDWARD P. OFFUTT, JR., AND O. R. MCCOY*

Trichinella spiralis is noted for its ability to parasitize a wide variety of hosts. Experimentally, it is able to develop in all species of mammals that have been tested and even in certain birds (1, 2). Although the course of infection has been studied quantitatively in only a few animals, it is apparent that the parasite exhibits different degrees of pathogenicity in different hosts. Thus, rats are relatively insusceptible and readily develop a high degree of resistance to reinfection (3, 4), whereas guinea pigs (5, 6, 7) and monkeys (8), are relatively susceptible and are killed by comparatively small doses of larvae. Compared to rats, these animals develop only a slight degree of resistance to reinfection.

The purpose of the present experiments was to test the susceptibility of the "gopher," *Citellus richardsonii* (Sabine), to infection by *Trichinella spiralis* and to measure the ability of this host to develop resistance to reinfection.

MATERIALS AND METHODS

The experimental host, *Citellus richardsonii* (Sabine), commonly called the "gopher," is a small rodent which is widely distributed in the North Central States and the adjacent parts of Canada. The adult animals vary in weight from 400 to 1000 gm. They live in burrows in pastures and fields. They are usually herbivorous, but may be sufficiently carnivorous to devour sick or weakened members of their own or related species. As far as the writers are aware, *Citellus richardsonii* (Sabine) has never been reported as a natural host for *Trichinella spiralis.*

The animals used in the present experiments were captured in North Dakota. In the laboratory they were confined in metal cages and fed a diet of commercial dog chow. They were infected by the administration through a stomach tube of *Trichinella* larvae that had been obtained by digestion from the muscles of infected rats. The methods used for counting the adult worms and the encysted larvae in the infected animals were similar to those used in earlier experiments with rats (3). (The counts of adult worms include the worms found in the cecum and large intestine as well as those present in the small intestine. Comparatively few worms, usually less than 10 per cent, were found in the former location.)

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EXPERIMENTAL

Twenty-three "gophers" were infected with from 2 to 40 *Trichinella* larvae per gm of body weight (Table 1). Five of them (No. 1, 2, 4, 17, and 18) died within 4 weeks, before it was possible to make an accurate count of the number of larvae in the muscles. Seven other animals were reinfected in order to test their resistance, thus interfering with the determination of the number of adult worms present in the intestine as a result of the first dose of larvae. The data for the remaining 11 animals are complete.

TABLE 1.—*Course of infection in "gophers" that were fed from 2 to 40* Trichinella spiralis *larvae per gram of body weight*

"Gopher" No.	Larvae per gm of body weight	No. of larvae fed	Died — days after infection	No. of adult worms in intestine	Per cent of larvae fed	No. of larvae in muscles	Ratio to infecting dose
			Experiment 1				
1	40	24,400	4	12,860	53	.....	...
2	40	12,400	16	2,720	22	.....	...
3	40	17,200	31	2,960	17	2,810,000	163
4	20	12,800	5	7,200	56	.....	...
5	20	13,600	31	1,340	10	1,670,000	123
6	20	12,800	72*	0	0	2,313,000	181
7	10	4,800	77	210	4	1,778,000	370
8	10	5,800	80	.....†	..	1,815,000	313
9	10	6,200	79	.....†	..	1,671,000	270
10	5	2,550	98*	.....†	..	978,000	383
11	5	2,600	105*	.....†	..	898,000	345
12	5	3,300	91	40	1	1,418,000	430
13	2	1,100	58	240	22	1,028,000	935
14	2	960	98*	.....†	..	233,000	243
15	2	1,000	105*	.....†	..	937,000	937
16	2	980	95	.....†	..	620,000	632
			Experiment 2				
17	5	3,150	14	1,720	54	.....	...
18	5	3,650	23	2,440	67	.....	...
19	5	3,680	37	2,170	59	1,900,000	521
20	5	2,150	39	2,150	51	1,613,000	750
21	5	4,300	56	870	20	1,678,000	390
22	2	1,020	31	340	33	460,000	451
23	2	1,020	70	0	0	438,000	430

* Animals that were killed.
† Reinfected before death.

Each of the 23 "gophers" used became infected with the parasite and each, with only one or two exceptions, showed a marked loss of weight during the course of the experiments. Substantial numbers of adult worms were found in the intestines of nearly all of the animals that died or were killed at a time more than 4 weeks after infection. Thus, two "gophers" (No. 13 and 21) that died after 8 weeks harbored 240 and 870 worms, respectively, representing 22 and 20 per cent of the numbers of larvae fed. In two instances (No. 12 and 16), a few worms still persisted 13 weeks after the feeding of the larvae. As far as the writers are aware, this is the maximal length of life that has been reported for adult trichinae in any host.

A measure of the susceptibility of a host to *Trichinella* infection is provided by the ratio of the number of the larvae that encyst in the muscles to the number of the larvae that were originally fed. In 18 of the "gophers," this ratio showed great variation, the range being from 123 to 937 times the infecting dose and the average 437 times. Part of this variation may be explained by the fact that many of the animals died while invasion of the muscles was still taking place, thus permitting the young larvae that had not yet encysted to be lost during the process of digestion.

Five "gophers," which survived for 13 weeks after the initial dose of larvae, were fed a second dose of from 2 to 5 larvae per gm of body weight. One animal died and the others were killed within 2 weeks after the second infection. All of them showed numerous adult worms in their intestines, representing from 40 to 100 per cent of the larvae fed in the second dose. Two other "gophers" (No. 8 and 9) acquired a second dose of larvae accidentally by feeding upon the carcass of an infected "gopher" that had died in their cage. Both animals died within 3 days and were found to harbor 15,400 and 11,530 adult worms, respectively. These few tests discouraged further reinfection experiments, because it seemed evident that any immunity that could be demonstrated in "gophers" would be insignificant as compared to the high degree of immunity developed by rats. It is possible, however, that some resistance to reinfection might be demonstrated in "gophers" if smaller test doses were fed to animals that had had a longer time in which to recover from the initial infection.

DISCUSSION

From the data available, as Roth (6) has pointed out, guinea pigs, monkeys and humans appear to be the most susceptible hosts to *Trichinella* infection, whereas rats, mice, rabbits and swine are relatively insusceptible. The present experiments indicate that the "gopher," *Citellus richardsonii* (Sabine), is also a host that is very susceptible to trichiniasis. Ten of 14 animals died following infection with doses as small as from 2 to 5 larvae per gm of body weight. Adult worms, furthermore, persisted in the intestines of the "gophers" for longer periods of time than have been reported for other hosts, the maximal period observed being 13 weeks. The ratio of the number of the larvae encysted in the muscles to the number of the larvae fed averaged 437 in 18 "gophers." This figure is much lower than that for guinea pigs (approximately 1,000 (6)) or for monkeys (700 (8)), but it is higher than the ratio for rats (100 to 200, depending upon the size of the initial infection (9)). The low ratio in the "gophers," as compared to the ratios found in guinea pigs and monkeys, may be explained by the fact that on the average only about 50 or 60 per cent of the larvae fed to the "gophers" became established in the intestine as adult

worms, whereas this percentage is usually greater in the other two hosts mentioned.

SUMMARY

The "gopher," *Citellus richardsonii* (Sabine), was found to be very susceptible to infection with *Trichinella spiralis*. Ten of 14 animals fed doses as small as from 2 to 5 larvae per gm of body weight succumbed. Adult worms persisted in the intestines of most animals for long periods of time, 13 weeks being the maximal period observed. Five "gophers" that were reinfected showed no resistance to the test doses of larvae that were employed.

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RESEARCH NOTES

A CASE OF CORRELATION BETWEEN INFECTION OF SNAIL HOSTS WITH *CRYPTOCOTYLE LINGUA* AND THE HABITS OF GULLS

During the summer of 1939, the writer, while at the Isles of Shoals Marine Biological Laboratory, had the opportunity of examining a large number of *Littorina littorea* for the immature stages of trematodes. The snails were secured from Duck Island, Appledore Island, and Smuttynose Island of the Isles of Shoals group off Portsmouth, N. H., and from Boone Island, Maine. In all, 817 snails of the species *Littorina littorea* were examined. Of this group, 75 were infected with immature stages of *Cryptocotyle lingua,* a common trematode of gulls.

A tabulation of the results of the examination of these snails shows that there is a correlation between the percentages of infected snails from various areas and the relationship of the gulls to these same areas. In areas where there are docks from which the gulls are continuously frightened, the writer found no *L. littorea* infected with *C. lingua.* On the other hand, in the feeding areas of gulls, six collections involving a total of 501 snails showed 6.2% of the snails infected. In the individual collections of this group, the percentages ran from 3.2% to 8.4%. The highest incidence of *C. lingua* in *L. littorea* is found near roosting and nesting sites of the gulls. Of the 86 snails examined from roosting areas, 17 or 19.8% were infected. A slightly higher incidence of infection, 20.9%, was found in the 134 snails examined from two nesting sites. In one nesting area, where the colony is small and somewhat scattered, the incidence ran only 14.3% while 30.0% of the snails from Duck Island were infected. Here the colony is large and crowded.

The localization of areas showing different percentages of infection of *C. lingua* in the snail host is in agreement with Stunkard's assertion (1930. J. Morphol. and Physiol. **50**: 143–191) that there are in this species no free-living miracidia but that the eggs containing mature larvae are ingested by snails and the miracidia escape within the intestine of the snail. If there were free-living miracidia, one would not expect such a distinct difference in rate of infection between areas in many instances only a few hundred yards apart. The writer found that when fecal material from infected gulls was squirted against sea-lettuce or other marine vegetation, the eggs often adhered to such material. *L. littorea* ingested large numbers of the eggs when kept in aquaria with vegetation contaminated with fecal material from infected gulls. Thus it is probable that eggs contained in gull feces adhere either to the rocks or to the vegetation and that many of these eggs are eventually ingested by the snails. Such a contention would account for the fact that the miracidia apparently are not washed about by the waves. If they were carried about by the waves and currents or were capable of locomotion, one would expect a rather uniform distribution of the infection in snails over a large area.—C. Clayton Hoff, *Urbana, Illinois. Contribution from the Zoological Laboratory of the University of Illinois, No. 588.*

THE HELMINTH FAUNA OF A RACCOON

In August, 1940, on the Edmund Niles Huyck Preserve, Rensselaerville, Albany County, New York, a male raccoon, *Procyon lotor lotor* (Linnaeus), of approximately 12 pounds weight was trapped, and its alimentary and circulatory systems examined for parasites. The locations from which the parasites were taken in the alimentary canal were noted to see whether quantitative data could be gathered to show that certain regions of the digestive tract were preferred over others.

Two species of helminths, a nematode, probably *Physaloptera maxillaris,* and a tapeworm, *Mesocestoides* sp., were removed from the alimentary canal. The distribution of the former was as follows: 29 individuals in the region of the greater curvature of the stomach, 11 individuals 6 inches down the small intestine from the

pyloric sphincter, and one individual 12 inches down the intestine from the pyloric sphincter. The preference for the stomach bears out the statement of Hall (1916, Proc. U. S. Nat. Mus. **50**: 212) concerning the region of the alimentary canal preferred by members of the genus *Physaloptera:* "Parasitic in the digestive canal, especially the stomach, of mammals, birds, and reptiles."

Sixteen individuals of *Physaloptera* were removed from the postcaval vessel of the circulatory system. The presence of these individuals in the circulatory system is apparently abnormal, since members of this genus are typically parasitic in the alimentary canals of reptiles, birds, and mammals.

Fifteen individuals of the genus *Mesocestoides* were distributed in the small intestine in a zone from 15 to 20 inches above the point of union of the small intestine with the large intestine.

Acknowledgment is made to Dr. Benjamin Schwartz, Washington, D. C., for identifying the two helminths.—William Marcus Ingram, *Zoological Laboratory, Cornell University.*

HEMATOZOA FROM CALIFORNIA BIRDS

In the course of routine examination of a series of 55 birds collected about the Los Angeles area blood smears and impression preparations of internal organs were studied. In addition smears of the peripheral blood of 75 birds caught for banding purposes on the campus of the University of California at Los Angeles were examined. The following summary is a record of the types of parasites and the numbers of infected birds found in the course of this survey:

Haemoproteus

Brown towhee (*Pipilo crissalis senicula*) (12), California jay (*Aphelocoma californica californica*) (7), western mourning dove (*Zenaidura macroura marginella*) (3), spotted towhee (*Pipilo maculatus megalonyx*) (2), Gambel sparrow (*Zonotrichia leucophrys gambeli*) (2), California thrasher (*Toxostoma redivivum*) (1), California quail (*Lophortyx californica vallicola*) (1), Cooper hawk (*Accipiter cooperi*) (1).

Plasmodium

California thrasher (3), California jay (3), western mockingbird (*Mimus polyglottos leucopterus*) (1).

Leucocytozoon

California jay (4), California thrasher (2), brown towhee (1), screech owl (*Otus asio*) (1).

TRYPANOSOME

Brown towhee (2), California jay (1), long-tailed chat (*Icteria virens longicauda*) (1).

MICROFILARIA

Brown towhee (7), California thrasher (5), California jay (3), white-rumped shrike (*Lanius ludovicianus excubitorides*) (1), pallid wren-tit (*Chamaea fasciati henshawi*) (1), ash-throated flycatcher (*Myiarchus cinerascens cinerascens*) (1), screech owl (1).

One pallid wren-tit was infected with a parasite of undetermined nature which was found only within the monocytes. This parasite, which resembled closely the haemogregarines of lower forms, seemed to be particularly abundant in the heart blood.

The following birds were examined but recorded as negative: California quail (28), brown towhee (13), pallid wren-tit (5), spotted towhee (4), California thrasher (4), western mourning dove (2), Gambel sparrow (2), western tanager (*Piranga ludoviciana*) (2), cactus wren (*Heledoytes brunneicapillus couesi*) (2), white-rumped shrike (2), California jay (2), hermit thrush (*Hylocichla guttata*) (2), song sparrow (*Melospiza melodia*) (2), western mockingbird (2), bush-tit

(*Psaltriparus minimus minimus*) (1), phainopepla (*Phainopepla nitens*) (1), horned-lark (*Otocoris alpestris*) (1), golden-crown sparrow (*Zonotrichia coronata*) (1).

There was a much higher infection (60 per cent) found in those birds in which complete examination was made, as compared with the infection (18 per cent) found in those birds in which only peripheral blood was examined. Similarly, 17 infections with more than one parasite were recorded for those birds which were completely examined, whereas no cases of multiple infection were recorded from those birds from which only peripheral smears were examined.

From this survey the following are considered new host records:

Haemoproteus: Brown towhee, spotted towhee, Cooper hawk, Gambel sparrow, California thrasher.

Plasmodium: California thrasher, western mockingbird, California jay.

Trypanosome: Brown towhee, long-tailed chat, California jay.

J. Frederick Wohnus and Dwight L. Ryerson, *Department of Zoology, University of California at Los Angeles.*

PARAGONIMUS IN A CAT FROM NORTH CAROLINA

Two specimens of *Paragonimus kellicotti* have been found in a cat from eastern North Carolina. Both were adults, one lying free in the thoracic cavity, and the other embedded in the lung tissue. No young specimens could be found, either in the lungs or in other parts of the body. As far as is known to the writer this is the first time *Paragonimus* has been reported from this state, although Smith (1911, Proc. Path. Soc. Phila., N. S. **14**: 64) has found the adults in a wild cat from South Carolina. Metacercariae have been found in crayfishes from Virginia and West Virginia by La Rue and Ameel (1937, J. Parasitol. **23**: 282).—A. B. Hardcastle, *Department of Zoology, Duke University, Durham, North Carolina.*

THE POLYCLAD, *HOPLOPLANA INQUILINA THAISANA* PEARSE, 1938, FROM THE MANTLE CAVITY OF OYSTER DRILLS

In May, 1938, a small turbellarian was detected in the mantle cavity of the oyster drill, *Urosalpinx cinerea* Say. Dr. Libbie Hyman has kindly identified this form as *Hoploplana inquilina thaisana* Pearse, 1938. Similar worms were later obtained from the rarer gastropod, *Eupleura caudata* Say. Specimens have been obtained from oyster drills from a number of areas within the oyster-growing regions of Delaware Bay.

In studying the distribution and incidence of this worm the oyster drills are brought to the laboratory where they are crushed and the soft parts removed and placed in beakers of sea water in lots of 30–50. The turbellarians soon leave the drill meats and climb the sides of the beaker from whence they are taken for isolation and study. This method has objections in that all worms may not climb up the sides and because multiple infections are missed. Since the latter are relatively few in number this is not a serious omission, and if the data are used only for determining relative incidence the former objection is also minimized. Using the above method 7,886 *Urosalpinx* were crushed in the past 3 years yielding 266 *Hoploplana* or 3.4 for every 100 drills crushed. From 494 crushed *Eupleura* only 6 specimens or 1.2 per 100 were obtained. A number of the *Urosalpinx* (640) were examined individually immediately after crushing by opening the mantle cavity and searching for worms, and 28 were found to be infected. Twenty-four of these (89 per cent) had only one *Hoploplana* in the mantle cavity, 3 had 2 worms and only 1 had 3 worms. There were 33 lots of drills crushed with worm incidence varying from none in a lot of 400 drills to 18 in a lot of 60 drills. Likewise the incidence varied from 0 in some parts of the bay to 10 worms per hundred drills crushed in drills collected from other areas. Heaviest incidence occurred in drills taken from a station along the Cape May Shore of Delaware Bay in the tidal zone. Drills from deeper waters seem to be either lightly attacked or to have no worms at all.

The turbellaria are oval and flat ranging in size in the living from 0.6 × 0.3 mm to 5.0 × 3.0 mm, most specimens being from 1–3 mm long and about three-fourths as wide. There are conical tentacles with clusters of tentacular eye spots in and around the bases of the tentacles and cerebral eye spots in 2 clusters more anteriorly. The number of tentacular eye spots varies significantly with the size of the turbellarian, totalling only 7 in a worm 0.8 × 0.6 mm. There were 34 in a worm 3.1 × 2.7 mm. The penis has a small pointed stylet and the uteri are not united anterior to the pharynx. Uteri distended with ova were seen in the larger specimens in the late spring and summer of 1939 and 1940. In June and July, 1939, and September, 1940, oviposition occurred when the turbellaria were isolated in watch glasses containing sea water, the egg masses being laid in a single or occasionally double coiled string. In 4 batches counted there were 144, 342, 245 and 50 eggs. The ova in one batch measured 74–81 μ and in another 89–95 μ in diameter.

The salinity of the water from which the *Urosalpinx* were obtained usually ranges from 18–25 parts per mille. When live and uninjured oyster drills were being experimentally studied for death rate and survival in test waters of low salinity (9–11 p.p.m.) it was noted that the *Hoploplana* infecting them would abandon the host under these unfavorable conditions and could be found on the glass walls of the container. This phenomenon occurred in salinities of 6, 7, 8, 9, 10 and 11 p.p.m. There is evidence that the turbellarians were injured by these conditions and frequently appeared moribund when discovered.

The genus *Hoploplana* now has representatives in the Eastern United States in *Busycon* from the Woods Hole area (1894, Wheeler, J. Morph. 9: 195–201) in *Tethis* taken from Apalachicola Bay, Florida (1938, Pearse, Proc. U. S. Nat. Mus. 86: 67–98) and in *Urosalpinx* and *Eupleura* from Delaware Bay reported here. The New Jersey and Florida specimens agree in size and are both smaller than the Woods Hole specimens.

Busycon from Delaware Bay uniformly have been found free from this genus of polyclad.

Much of interest would arise from studies of these molluscs and their mantle cavity commensals throughout their geographic range.

Assistance in the preparation of these materials was furnished by the personnel of Work Projects Administration, Official Project 265-1-22-477.—LESLIE A. STAUBER, *Oyster Research Laboratory, N. J. Agricultural Experiment Station, Bivalve, New Jersey.*

NEW NAMES FOR *METABRONEMA SALVELINI* FUJITA AND *CYSTIDICOLA MINUTA* FUJITA

Dr. Benjamin Schwartz of the United States Bureau of Animal Industry has kindly called my attention to the fact that *Metabronema salvelini* Fujita (1939, J. Fac. Agric. Hokkaido Imp. Univ. **42**: 239–260) was preoccupied by *M. salvelini* (Fujita, 1922) Baylis (1935, Ann. and Mag. Nat. Hist. 10 s. **16**: 378–380), and *Cystidicola minuta* Fujita (1940, Jap. J. Zool. **8**: 377–394) by *C. minuta* Rodhain and Vuylsteke (1934, Rev. Zool. et Botan. Africaines **24**: 406–409). Accordingly, I wish to propose for these homonyms the new names *Metabronema ishii* and *Cystidicola chika* for *M. salvelini* Fujita and *C. minuta* Fujita, respectively.—TSUNENOBU FUJITA, *Faculty of Agriculture, Hokkaido Imperial University, Sapporo, Japan.*

GENUS NAME *MARTINEZIA* CHANGED TO *MARTINEZIELLA*

We have been informed by Dr. Enrique Beltran that the genus name *Martinezia*, which we proposed for a species of ameba discovered in the intestine of an iguana, *Ctenosaura acanthura* (J. Parasitol., 1940, **26**: 319–321), has already been used for an orthopteron. We now propose the genus name *Martinezella* in place of *Martinezia*.—ROBERT HEGNER AND REGINAL HEWITT, *Instituto de Salubridad y Enfermedades Tropicales, Mexico, D. F.*

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